THE FUNCTION OF ROLL IN FORAGING BEHAVIOUR OF SPERM WHALES

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Abstract

Though direct experiments to test echolocation in sperm whales (Physeter macrocephalus) remain impossible, the indirect evidence is overwhelming that one function of their clicks is echolocation used during foraging, as has been shown for other toothed whales. In this thesis, the aim was to test: 1) the hypothesis by Fristrup and Harbison (2002) that the sperm whale might be using downwelling light during the day to spot prey or prey patches as silhouettes against the lighter sea surface. 2) A second hypothesis by Fristrup and Harbison (2002) suggested that the sperm whales use vision to look for bioluminescence in prey at depth, or during the night when no light is available. 3) Indications that the sperm whales changed their roll-behaviour, rolling more extensively when they were producing regular clicks during the descent as well as for the ascent. Data from 51 sperm whales tagged in the Gulf of Mexico, the Atlantic, the Mediterranean and northern Norway, were tested to explore how large a proportion of the bottom-interval the whales spent at angles where they were able to see towards the lighter sea surface at three different pitch-modes while either searching or buzzing, for each dive. The majority of whales were found to be swimming predominantly upside down or on the side during both the day and night time. The whales were not found to change the way they use roll at night compared to the day time, when looking at the bottom-interval when the whales were both searching for prey and buzzing.

Looking at another function for roll and a possible association with the echolocation of the sperm whales, it was found that during the descent, the whales had a tendency to have a higher variance of roll when they were producing regular clicks. A very similar trend showed for the ascent-phase as well, that they seemed to roll more when clicking compared to when they were not, before they reached the sea surface. These analyses of the roll-behaviour of sperm whales used to test the hypotheses put forward by Fristrup and Harbison do not seem to support the use of vision to detect prey during foraging at depth, but might indicate that the sperm whale was intentionally changing its roll-behaviour, when they were producing regular clicks during the ascent and descent-phase in the Gulf of Mexico, the Atlantic, the Mediterranean and Norway.

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CHAPTER 1: General Introduction

1.1 Dive behaviour

Sperm whales (*Physeter macrocephalus*) are a cosmopolitan species, and they usually forage in mesopelagic and benthic habitats. Their primary prey is medium-size, bioluminescent, neutrally buoyant squid, but remains of fish have also been found in stomach contents of whales in many locations, including the North Sea (Santos et al. 1999), New Zealand (Gaskin and Cawthorn 1967) and off the Azores (Clarke et al. 1993). Sperm whales have been estimated to consume approximately 1000 squid per day, from the analysis of flesh-remains and beaks in stomachs of commercially caught sperm whales off the Azores (Clarke et al. 1993). The ability to catch such a large number of prey items is supported by the fact that sperm whales spend over 50% of their time actively foraging for prey (Watwood et al., 2006).

Sperm whales, as other toothed whales, use echolocation to investigate the environment and to find prey. Sound is a very important medium in water, especially in deep water where light is often limited. As with other deep diving species, it has been a difficult task to investigate details of how sperm whales forage at depths of 200-2000 m. Previous studies have been done using hydrophone arrays from boats (Jaquet et al. 2000, Madsen et al. 2002, Teloni 2005) to determine the whale's position, depth and the sounds produced. These studies also focused on getting an indication of the whale's diving behaviour: how do they forage and at what depths. Recently, the use of archival tags, such as the d-tag (Johnson and Tyack, 2003) have allowed for more detailed monitoring of entire dives by recording acoustic data, depth, roll, pitch and heading of the whale simultaneously while at depth.

Madsen et al. (2002) found that regular clicks produced with a centroid frequency at around 15 KHz are highly directional and very useful to locate groups of squids at a distance up to 500 m. In a more recent study, Madsen et al. (2007) found that the target strength was primarily affected by the muscles and fins of the mid-size longfin squid (*Loligo pealeii*). They estimated that a sperm whale would be able to detect squids of this

species at a distance of 100-325 m depending on the background noise and the position of the squid. The estimated distance of detection would increase for more muscular and larger species, maybe even to a distance of up to 1000 m for a jumbo squid, under low noise conditions at depth. Neutrally buoyant deep sea squids on the other hand would be more difficult to detect, especially a single animal, which they estimated could be detected at a range of 60 m under low noise conditions, a patch of these neutrally buoyant squids might give a better backscatter than just a single animal, but will probably not be detectable at greater distances (Madsen et al., 2007).

Foraging dives of sperm whales, as defined by Watwood et al. (2006), are deep dives with dive depths over 300 m with the presence of buzzes, which by now are recognised as an indication of a prey-capture or at least an attempt to catch a prey item (Jaquet *et al*, 2000; Madsen et al., 2002; Miller et al., 2004a). Watwood et al. (2006) also reported that tagged whales in the Atlantic and the Gulf of Mexico spent 72% of their time on foraging dives, while tagged whales in the Ligurian Sea spent almost all of their time (97%) on the same type of deep dives (Watwood et al. 2006). Sperm whales off Japan showed the same pattern, with the tagged whales spending 77-80% on deep foraging dives (Amano & Yoshioka 2003). During such deep dives which have been monitored acoutstically, the whales have been found to almost continuously produce regular clicks interrupted from time to time by buzzes. After each buzz there is usually a 5-20 second period of silence (Madsen et al., 2002) before the regular clicks are produced again. Sperm whales stop clicking at variable depths during ascent from depth (Watwood et al., 2006; Teloni et al., 2008).

1.2 Diet

Sperm whales are considered to be opportunistic feeders, rather than specialists on any particular prey type. Nonetheless, their diet seems to be dominated by mid-size neutrally buoyant cephalopods, with fish being a part of their diet as well as shown for different locations around the world (Gaskin & Cawthorn, 1966; Clarke, 1980; Clarke et al., 1993; Clarke et al., 1996; Evans & Hindell, 2004). Because feeding events usually takes place at depth, it is difficult to document exactly what they eat, and how they capture their prey. Occasionally people have witnessed pieces of squid coming to the surface in the

area where sperm whales later appear, are heard on a hydrophone or have been seen to fluke out, setting off into a deep dive. Another way of testing what the whale is eating is by collecting and analysing faecal samples (Smith and Whitehead, 1999). The most successful method, which has provided the most information about what is being eaten by these giant mammals thus far, is analysis of stomach contents of commercially caught whales during the whaling cruises, or from stranded animals.

By analysing the stomach contents of sperm whales caught commercially through whaling in New Zealand, Gaskin & Cawthorn (1966) found that cephalopods were clearly the main prey of these sperm whales, though they did find quite a number of fish remains in the stomachs as well. This is supported in Evans & Hindell (2004) who found that the main prey item in 36 stranded sperm whales in Tasmania, Australia, was subtropical muscular cephalopods. The cephalopod species found were thought to have depth ranges throughout the entire water column. Cephalopod beaks were found in all of the stomachs, fish parts were present in 16.7% and parts of crustacean exoskeleton found in 44.4%. There seemed to be a difference in prey distribution between males and females, with the majority of the prey found in the stomachs of males being Antarctic species, whereas the remains of tropical or subtropical species were usually found in stomachs of female sperm whales. The immature animals in the study by Evans and Hindell (2004) showed a prey distribution somewhat in-between the males and females with species mainly from the subtropics and Antarctic. Another gender difference was the occurrence of fish, which was found in half of the males, but only 10% of the females. Fish remains were found in 93 of the 133 sperm whales caught in New Zealand (Gaskin & Cawthorn, 1966), where species like Groper (*Polyprion oxygeneios*), a deep sea fish, were regularly found in the stomachs, which would indicate foraging depths of 370-854 m depth, where these fish are usually found (Barreiros et al., 2004).

In many parts of the world, especially in the temperate and tropic areas, the *Histioteuthids*, a neutrally buoyant, gelatinous and slow group of squid species, have been found to be one of the major prey species based on faecal samples in the Galapagos Islands (Smith & Whitehead, 1993). Clarke et al. (1996) found the same species to take up a large part of the total mass of the stomach content, even though they are not particularly large in size, the numbers found in the stomachs were great. This species is

usually considered a pelagic species, and in Watanabe (2006) the species were found at depths between 500-700 m, though they have been shown to venture close to the seabed as well (Vecchione & Roper, 1991).

Another main prey species is the Ommastrephids which includes the jumbo squid (*Dosidicus gigas*) that have been found to be a dominant prey species, especially for the sperm whales found in the Gulf of California. Here a mature jumbo squid can grow up to 2.5 m long and weigh 50 kg (Gilly et al., 2006). This species is muscular and fast and usually lives in the mesopelagic zone from 200-1000 m and is an important species linking lower trophic levels with top predators, like the sperm whale (Davis et al., 2007). In one study where these large squids were tagged, Davis et al. (2007) found that the squid dove to depths of 500 m, but usually spend most of their time at depths between 200-400 m during the day. Gilly et al. (2006) also found that the *G. gigas* spend much of their time at depths deeper than 200 m during the day which corresponds with the deep Scattering Layer at 200-300 m and the top layer of the Oxygen Minimum Layer (OML). They spend a lot of time in the OML, which is highly unusual for an active and muscular species. By measuring the standard aerobic metabolic rate in the laboratory, Gilly et al. (2006) found that the jumbo squid can adjust its need for oxygen depending on the environment around it, by lowering the rate of oxygen consumption. This enables them to take advantage of the protection the low oxygen levels gives them from predators like many pelagic fish that do not tolerate the low oxygen levels as well. It has given the jumbo squid the advantage of being able to forage in both the oxygenated shallow waters as well as the OML with less competition (Gilly et al., 2006).

1.3 Diurnal migration

The Deep Scattering Layer (DSL) is found in a great majority of the oceans in different degrees, and divided into one or more layers, with one layer being the most normal (Tont, 1975). The animals in the DSL are influenced mainly by light, but have been shown to be affected by temperature as well, and usually start their vertical migration when the light intensity falls around dusk, moving from the depths towards the surface waters. Here,

nekton like fish and squid feed off the large mass of plankton that has moved to the surface and descend again around dawn to return to their day time depth at several hundred meters. Hays (2003) conclude that the primary reason for organisms to undertake the vertical migration is to avoid predators, especially those that use vision during the day. They stay at deeper depths during daylight hours and move to the surface to feed at night.

Some cephalopod species, including some found in stomach contents of stranded or commercially caught sperm whales, exhibit clear diurnal vertical migration. In a study by Watanabe et al. (2006) in the Warm Core Ring and the Cold water mass in the western North Pacific a number of subtropical and transition water species were caught in trawls at different depths during the day and at night. They found indications of both migrating and non-migrating species. Migrating species stayed at depths of 400-700 m during the day and at night they went to depths less than 100 m in both areas. They found a depth separation that matched the characteristics of the two different types of species. The vertically migrating species that usually require more energy to undertake the vertical migration, and most likely obtain that energy from the more variable and energetically favourable prey within the DSL, compared to the non-migrating species that are slower and gelatinous and has chosen a more energy saving foraging strategy (Watanabe et al., 2006). The more muscular Jumbo squid shows extensive vertical movement (Gilly et al., 2006; Davis et al., 2007). During the day they tended to stay at depths around 200-400 m, whereas at night they tended to stay shallower than 100 m though with deep dive excursions to 300-400 m on a regular basis after being at the surface. Gilly et al. (2006) and Davis et al. (2007) propose that these deep dives into cooler waters might be because of temperature stress caused by the higher temperatures at the surface, where they appear to be foraging.

Because many of the squids found in the stomachs of sperm whales are muscular, and could themselves take on a more active foraging strategy by feeding on fish and smaller squid in the DSL, it would be interesting to know whether sperm whales follow their prey into the shallower depths at night. Several studies have recorded data from both day and night time, giving them the opportunity to see if sperm whales are following the diurnal pattern of some of their prey. In Davis et al. (2007) they found that the average

dive depth of 462.5 m (± 303.1 m) during the day was deeper than the average depth of 381.0 m (± 128.3 m) at night for tagged sperm whales in the Gulf of California, but found no significant diurnal difference in the number of deep dives. Sperm whales off the coast of Japan were found to show some pattern of diurnal movement. Aoki et al. (2007) found that sperm whales dove to a significantly deeper depth, and at higher speeds during the day than was observed at night off the Ogasawara Islands in south of Japan. At their second study location, off the Kumano coast of Japan, they did not find any significant diurnal differences in dive depth or speed, though the dive depths were somewhat deeper during the day compared to the night time dives. Amano & Yoshioka (2003) also found that even though dive duration and the whale's behaviour during the dives showed no difference for day and night time dives, they did find a difference in dive depth, with dives to shallower depths during the night.

Baird et al (2005) found the opposite behaviour. Fish-eating killer whales (*Orcinus orca*) in Canada showed a lower number of deep dives during the night as well as slower swimming speeds, which could be a result of less available prey. The same tendency was found in Blainville's beaked whales (*Mesoplodon densirostris*) in Hawaii, where they dove shallower during dives at night compared to day-time dives and seemed to be using the mid-waters between 100-600 m more during the day and stayed shallower than 100 m during the night (Baird et al., 2006). Although the diving depth seemed to have changed, they concluded that the tagged whales where foraging as much during the day compared to the night time based on speed and dive duration (Baird et al., 2006).

Other marine mammals, like the Baikal seal (*Phoca sibirica*) show patterns of moving with their prey (Watanabe et al., 2004). They found the seals in Lake Baikal to be diving almost continuously throughout the tag deployment, and to be diving to shallower depths during the night, with increasingly deep dives performed during dusk and dawn. Another example is the Antarctic fur seal (*Arctocephalus gazella*) where Croxall et al. (1985) found a very clear pattern of diurnal vertical migration. At dawn the dives became gradually deeper, and all dives performed during the day were mostly deeper than 40 m. At dusk the dive depth decreases and 75% of the dives are performed at night with dive depths less than 30 m. The diurnal pattern of the Antarctic fur seal was found to match

the diel vertical migration of their main prey in the same area, the Antarctic Krill (*Euphausia superba*) (Croxall et al., 1985).

In the Gulf of California, simultaneous tagging of the sperm whale predator, and their Jumbo squid prey made it possible to investigate underwater predator-prey interactions, particularly to see if the distributions of how they used depth matched each other (Davis et al., 2007). Sperm whales and giant squid were tagged in the same area and the data showed that 91% of the dives performed by the sperm whales were to the same depth where the tagged squids were located, so the possibility that the sperm whales target this species, when foraging in the area, is likely (Davis et al., 2007). The Jumbo squid is very abundant in this area, and the fact that the sperm whales seemed to stay in the area during the tag-deployment, suggested that foraging in the area was successful (Davis et al., 2007).

1.4 Thesis aims

Dtag data analysed from 51 tagged sperm whales at four different locations indicates extensive roll-behaviour by sperm whales during deep dives. The function of this rolling behaviour, if it has one, is unknown, but suggestions have been made in the literature. One is that the sperm whale use vision when they look for prey using downwelling light and bioluminescence in their prey (Fristrup and Harbison, 2002). Another is that rolling behaviour relates to the use of echolocation to search for prey (Akamatsu et al., 2009). The goal of this thesis is to explore the possible function or functions of rolling behaviour in sperm whales by exploring: 1) indications based on the roll angle that sperm whales might or might not use vision during foraging, and 2) the possible influence the use of echolocation will have on rolling-behaviour.

CHAPTER 2: Do sperm whales use vision when they forage at depth?

2.1 Introduction

Sperm whales have been found to make both shallow non-foraging dives and deeper dives where they produce buzz sounds, indicating foraging. Shallow dives have been defined in several studies as shallow dives of short duration usually performed in silence. Studies using the d-tag have shown dives with maximum depths of 150 m in which no sound was produced (Watwood et al. 2006). Similar shallow dives have been described by Jaquet et al. (2000), a study using a directional hydrophone, as dives with no fluke out, lasting less than 10 minutes and usually silent. In the Gulf of California, Davis et al. (2007) found that 74% of the dives recorded on a Satellite-linked Dive Recorder, were short shallow dives to 8-100 m depth that lasted less than 5 min. Interestingly, many dives recorded in Norway that would be considered 'shallow' in other locations contained clear indications of foraging, including regular clicks and buzz production (Teloni et al., 2008). Short, silent non-foraging dives recorded in Andenes, Northern Norway, showed a much shallower dive profile, usually at depths less than 25 m (Teloni et al. 2008).

2.1.1 Foraging

Foraging strategies can vary greatly within the marine environment, and odontocetes are known to use their very well developed echolocation to orientate and find their prey. But some may use sound in different ways, or may make use of other cues to aid their foraging success. In British Columbia, mammal-eating 'transient' killer whales are thought to use passive listening when foraging on porpoises, listening for their breathing sound when surfacing (Barrett-Lennard et al., 1996). A strategy of passive listening to find soniferous fish has been suggested to be used by bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (Gannon et al., 2005). Aguilar Soto et al. (2008) suggests that fast sprints performed by pilot whales in the Canary Islands, regularly

followed by an interval of slow descents, could resemble the stationary search and rapid prey capture-strategy used by bats and birds when hunting their prey using vision.

Sperm whales are opportunistic feeders, and in the case of limited food availability or an easily accessible prey item presenting itself, the sperm whales, as well as other marine mammal species, have been found to be very creative in their foraging strategies. Examples of this are of sperm whales picking black cod (*Anoplopoma fimbria*) off a longline in the Gulf of Alaska, with observations of a whale working the line with its jaw until the fish falls off (Mathias et al., 2009). In southern Chile, sperm whales and killer whales have both been linked to depredation of Petagonian toothfish (*Dissostichus eleginoides*), picking the toothfish off the line (Hucke-Gaete et al., 2004). They suggests that the sperm whales are most likely pulling or sucking the fish off the line by turning on their side or upside down based on the position of their mouth in relation to the rest of the head, leaving the lips of the fish still attached to the line. In the case of the killer whale, trunks or heads are left on the line, suggesting that the killer whales bites or tears the prey off the line (Hucke-Gaete et al., 2004).

Observations of depredation of fishing lines indicate that sperm whales are capable of elaborating diverse strategies to find and capture prey. Such flexibility indicates that sperm whales are like to use any available sensory modality to detect and capture prey. This thesis focuses on the possibility that they might use vision as a regular part of their foraging.

2.1.2 Light availability

Vision requires light, and natural sources of light include celestial sources (sun, moon, stars) which generate downwelling light in the ocean, and biological sources of light such as bioluminescence. At depths of 400-1200 m (Watwood et al. 2006) and 60-1860 m off Northern Norway (Teloni,et al. 2008), where sperm whales are known to forage, only a limited number of downwelling light photons might be available to support vision by sperm whales. In the mesopelagic zone, down to 1000 m, sunlight is scattered and absorbed all the way through the water column. How much, is dependent of the water quality; the presence of chlorophyll and Dissolved or Particulate Organic Matter

(Douglas et al. 1998). Typically, the intensity of light during the day falls tenfold for every 75 m increase in depth in oceanic waters (Denton, 1990). The Gulf of Mexico, The Ligurian Sea and the North Atlantic are all relatively clear waters, classified as Jerlov watertypes J1A, J1B and J1B respectively, where northern Norway is less clear and classified as a JIII (Jerlov, 1976). In the less clear waters in Norway, the minimum detectable light would reach depths of 200 meters, whereas detectable levels of sunlight would reach depth of 500-600 m in watertypes found at the remaining three locations, but to such a limited degree that it would be unlikely for fish at that depth to see (Douglas et al., 1998). Denton (1990) mentions that not even specialized deep sea eyes, with an adapted high sensitivity to light would be able to use the number of light photons left at a depth of 900 m. At this depth, bioluminescence may be the dominant light source. In the clear deep ocean water, the only light left after absorption and dispersal of the sunlight is the blue/green short wavelengths (<500nm) (Douglas et al. 1998, Warrant et al. 2003). Beyond the mesopelagic zone, exceeding 1000 m, insufficient light is thought to be available from downwelling light to be usable for vision (Warrant et al. 2003).

At such deep depths or during the night, the only light available for vision would be from the numerous bioluminescence-producing animals, which include several squid species that have been found in stomach contents from commercially caught sperm whales (Clarke et al., 1993). Bioluminescence is probably used by animals throughout most of the water column. Deep sea species use bioluminescence for a wide variety of purposes, among other things to communicate with mates, fight off rivals or to protect themselves from predators from the deep. To avoid being seen, many species use bioluminescent organs to make up for the down-welling light that their body shadows (Warrant et al. 2003), making the silhouette of their bodies against the lighter sea surface less detectable from below. Many bioluminescent species move in large parts of the water column, some by diurnal migration, but the greatest use of their bioluminescence may happen at depths over 1000 m where no daylight is present and contrast against the darkness is greater (Warrant et al. 2003).

2.1.3 Spectral sensitivity

Vision is generally used by many species in the marine environment. Most vertebrate retinae contain two photoreceptors; the cones and the rods. The rod-receptors absorbs photons at very low light levels, optimizing light sensitivity, where cones are better at perceiving details and colour at high light levels (Land, 1990; Douglas et al. 2003).

In cetaceans, Levenson & Dizon (2003) used nuclear DNA from 16 species, including sperm whales, to test whether or not they are lacking the visual pigment-cone-type: Short-Wavelength-Sensitive (SWS)-cones, as it has been shown in several delphiniid species (Peichl et al., 2001). In the Levinson & Dizon's (2003) study, they only found pseudo-genes for the SWS-cones for all the cetacean species tested, meaning that it is not possible to produce any functional genes for the visual pigment SWS. The loss of functional SWS-cones has made the whales and pinnipeds long-to-middle-wavelength-sensitive (L)-cone monochromats, and thus they lack cone-based colour vision (Peichl et al. 2001). But for deep diving species like the sperm whale, colour vision may be of less importance compared to better light sensitivity at depths with very limited light (Peichl et al., 2001). The majority of deep-sea fish also lack photoreceptor-cones (Douglas et al. 2003); that is, they have also adapted to light sensitivity instead of colour vision. Living at these depths, fish have adapted in the same way the deep diving whales have, both looking for food where light is limited. Southall et al. (2002) found that sperm whales have a "best pigment sensitivity" (λ_{max}) around 483 nm in the blue-green spectrum. This blue shifted 483 nm rod pigment, makes the sperm whale better adapted to use vision at depths down to 1000 m, by being more sensitive to short-wavelength blue light. As a comparison, deep-sea fish have been found to have vision adapted to the dim light at depths, with a visual pigment best sensitivity between 475-490 nm (Douglas et al. 2003) which is very similar, and may be a general adaptation for predators living and looking for prey at these depths.

2.1.4 Do sperm whales use vision while foraging at depth?

The use of vision when foraging is common in many terrestrial mammals. In marine mammals, foraging using vision as the primary strategy, could at times be a challenging task, with the water-quality varying, and thereby the visibility. One example is the suggested use of downwelling light when foraging in the Baikal seal, found to be accelerating from below the prey seen on video as a silhouette against the lighter sea surface in Watanabe et al. (2004).

Fristrup and Harbison (2002) set three alternative hypotheses for how the sperm whale might use vision while foraging at depth. One hypothesis "…postulates that sperm whales locate their prey visually, either silhouetted against the midwater 'sky', or by searching for bioluminescence produced by the movement of their prey" (Fristrup & Harbison 2002). A minor expansion of their hypothesis is that the whales are looking for active bioluminescence in their prey as well as for the bioluminescence produced by the movement of their prey. Fristrup and Harbison (2002) made predictions of how sperm whales should orient to make use of vision depending on the light source available.

The main variable of interest to test how sperm whales might use light during foraging is the proportion of time spent by whales swimming at angles where they are expected to be able to make use of the light effectively (Fristrup and Harbison, 2002). In the case of testing the use of downwelling light, the range of roll angles in which the whale can see upward includes more than just upside down swimming, but also swimming on the side. Clarke and Paliza (2003) have shown several examples of sperm whales thought to have been swimming upside-down when capturing their prey, based on the position of teeth marks in consumed prey. Their finding could be consistent with sperm whale use of downwelling light in foraging, but the bite marks might also reflect a preferred capture orientation with respect to escape behaviour of the prey. The study provides no indication of sperm whale orientations other than during prey capture, and does not consider that sperm whales can see upward at roll angles other than just upside-down.

To consider all the angles where the whale would be able to look toward the sea surface, the angles for when the whale is rolled on either side should be included as well.

Assuming that the sperm whales are not able to see above their head and to angles of 45 degrees either side when swimming flat, i.e. the roll and pitch are both 0º, because of the impairing eyefold sperm whales have above the eye. This means that when a sperm whale is rolled at angles between 45º and 315º it is predicted to be able to look towards the sea surface with at least one eye and spot silhouettes of single prey-items or prey patches against downwelling light. These roll angles will be referred to as "Looking Upwards Roll Angles" (LURA) see figure 2.1.

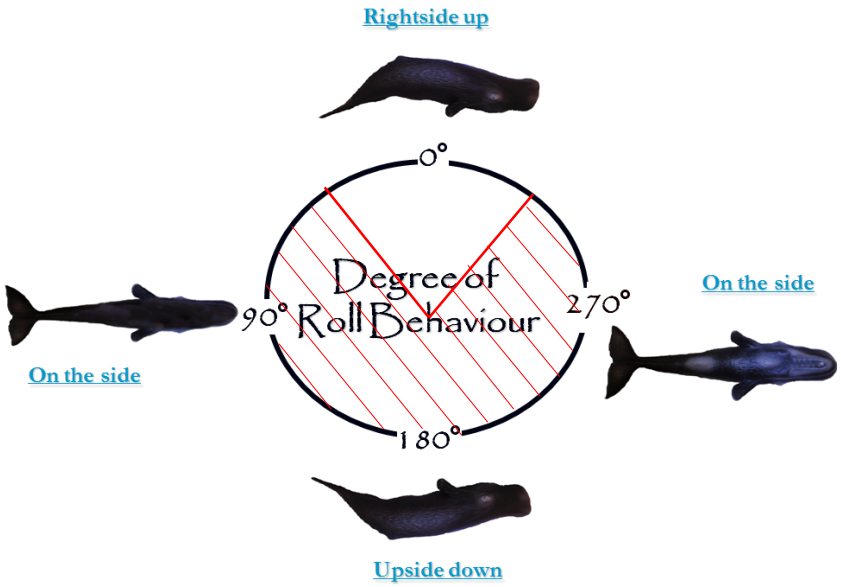

Figure 2.1 The 'Looking upward roll angles' (LURA), at which the whale is expected to be able to look towards downwelling sunlight from the sea surface using at least one eye are indicated by the red arrow, and correspond to the interval from 45º to 315º. Zero degrees indicate when the whale is swimming 'normally' or flat with dorsal side up, 90ºand 270º are when the whale is turned on either side and 180º is the whale turned upside down.

The proportion of roll measurements that fall within LURA, together with a mean depth constitute the data for each dive and show how much of the time in each of the pitch-modes for search and buzz phases during the bottom interval they spend at angles where they are thought to be able to look upwards.

Roll-behaviour will be examined during the buzz, as well as during search, to see if there is any indication that these whales might use vision during the final stages of prey capture.

The other visual strategy proposed for the sperm whale is to look for bioluminescence in their prey, which is found in a large part of known sperm whale prey species. Clarke at al. (1993) found that 77.5% of the squid species identified in stomach contents from sperm whales off the Azores had bioluminescent organs. Fristup & Harbison (2002) argued that "an upside-down posture would not be expected if sperm whales look for stimulated bioluminescence caused by the movement of their prey. The background will be darker below than above, so a 'normal' orientation would be favourable if the bioluminescent sources were omnidirectional". To test this, the data from dives performed at night, where no sunlight was present, will be compared to the daytime dives, to investigate whether there is any difference in roll manoeuvring that could indicate use of light by foraging sperm whales.

For the night time dataset it would be obvious to look at the whales manoeuvring to see if it shows a general difference in the proportion of upside down swimming compared to during the daytime. More swimming with the dorsal side up would be expected because of the lack of downwelling light. At night the whales do not have the possibility of using downwelling sunlight in the aid of prey capture, so a decrease in upside down swimming would be expected, and in relation to this of course an increase in normal dorsal side up swimming as described in Fristrup & Harbison (2002). Some prey species are diurnal migrants, so the prey might be dispersed more in the entire water column, making the prey patches less set than during the day. The whale might be doing more manoeuvring spread out over all angles to be able to visually detect a larger area of bioluminescent prey, visible against the dark background.

2.2 Materials and Methods

2.2.1 Data

The data analysed in this study are recordings from 51 sperm whales tagged in the Northern part of the Gulf of Mexico in July 2001, August-September 2002 and June 2003 (26 tag deployments); the Ligurian Sea in the Mediterranean in September–October 2001, July 2002 and September 2003 (11 tag deployments); the North Atlantic in July 2003 (7 tag deployments); and in Northern Norway in July 2005 and May and June in 2008 and 2009 (7 tag deployments). This combined dataset includes a total number of 371 full dives and 13 partial dives, in which the tag released from the whale at depth.

It was possible to confirm the gender for 9 of the tagged whales from skin samples from the Gulf of Mexico. They were all found to be females and immature males, except for one mature male (Miller et al., 2004b). The tagged individuals from northern Norway were all thought to be males based upon their large body size. The whales were observed and tracked from research vessels: R/Vs *Gorden Gunter, Gyre* and *Ewing* in the Gulf of Mexico, R/V *Alliance* in the Ligurian Sea, R/V *Delaware* in the Atlantic, and in Norway from the R/V *Iolaire* (2005) and H.U.S *Sverdrup* (2008, 2009). All whales were tagged with a digital recording tag, the Dtag (Tyack and Johnson 2003), using a 12 m pole from a small boat to attach the tag to the back of the whale with suction cups (for details on attachment and retrieval of the tag, see Miller et al. 2004b). After tag deployment the whale was monitored and located when at the surface by a VHF-tracking system, until the tag is released from the whale, either by the scheduled release or if the tag comes off prematurely.

The Dtag is a non-invasive digital recording tag attached using suction cups, and records both sound and sensor-data including pressure, depth, and the output of 3-axis accelerometers and magnetometers. The acoustic data was sampled at a sampling rate of 32 kHz (2001 and 2002) and at 96 kHz in 2003 with a 12 and a 16 bit resolution analogue-to-digital converter. The sensor-data was recorded with a sampling rate of 58.8 Hz in 2001 and 2002 and 50 Hz in 2003 and onwards, and then down-sampled by a factor 10 for further analysis. The pressure data was converted into meters by using calibrated

values, and the sensor data from the 3-axis accelerometer and 3-axis magnetometer were converted into roll, pitch and heading as described in Johnson and Tyack (2003) and Miller et al. (2004b). All data processing and analyses have been performed in Matlab versions 6.5 and 7 (Math Works).

To distinguish between day and night dives, the times for sunrise and sunset have been used for that particular longitude, latitude, date and year for each of the tags (Civil Twilight is used from http://aa.usno.navy.mil/data/docs/RS_oneyear.html). Separating the dives into night and day time, 310 full dives and 12 partial dives were recorded during the day time, and 57 full dives and 9 partial dives at night. Some of the dives are split by the time of sunset, and have therefore been separated into and analysed as one half day time and one half night time dive. Details for each of the tags are shown in table 1 for each of the four locations, giving time of day the tag was attached to the whale and for how long. As well as the number of full and partial dives for each of the tagged whales.

The majority of the tags have recorded data during the day, but two whales, both from the Gulf of Mexico, only have night time dives. Some have dives recorded from both day and night time, and at two locations, the Atlantic and northern Norway, they only have recorded day time data, but for two different reasons: in the Atlantic, the tags were released from the whale before sunset, whereas the sun in northern Norway never sets in the summer. Sunlight is available 24 hours a day because of the high latitudes north of the Polar circle.

Table 2.1 Summary of the tag and dive information from 26 whales in the Gulf of Mexico (GoM), 7 whales from the Atlantic, 11 from the Mediterranean and 7 whales from Norway. The tag-on time is the date and time of day the whale was tagged and tag on animal total time is number of hours and minutes the tag was on the animal.

Location	Tag-ID	Tag-on time	sex	Total # of dives	Day/Night data
GoM	**sw01_200**	19/07/2001 15:58	Female	8+1 part	Day + Night
GoM	**sw01_204**	23/07/2001 14:18	Female	6	Day
GoM	**sw01_208b**	27/07/2001 16:42	Male	1	Day
GoM	**sw01_209c**	28/07/2001 13:58	-	4	Day
GoM	**sw02_235c**	23/08/2002 17:03	Female	1+1 part	Day
GoM	**sw02_237a**	25/08/2002 11:23	Female	2	Day
GoM	**sw02_238a**	26/08/2002 09:22	Female	3+1 part	Day
GoM	**sw02_238b**	26/08/2002 16:23	-	3	Day
GoM	**sw02_239a**	27/08/2002 10:40	Female	12+1 part	Day + Night
GoM	**sw02_239b**	27/08/2002 17:38	-	1	Day
GoM	**sw02_240a**	28/08/2002 11:34	-	1	Day
GoM	**sw02_240c**	28/08/2002 17:03	-	5	Day + Night
GoM	**sw02_248a**	05/09/2002 18:11	-	1	Night
GoM	**sw02_249a**	06/09/2002 08:45	-	2	Day
GoM	**sw02_253a**	10/09/2002 16:38	-	3+1 part	Day + Night
GoM	**sw02_254a**	11/09/2002 11:09	Female	11+1 part	Day + Night
GoM	**sw02_254b**	11/09/2002 10:28	Female	9	Day + Night
GoM	**sw02_254c**	11/09/2002 10:34	-	10	Day + Night
GoM	**sw03_156a**	05/06/2003 10:06	-	5+1 part	Day
GoM	**sw03_162a**	11/06/2003 17:26	-	1	Day
GoM	**sw03_163a**	12/06/2003 17:54	-	2	Day + Night
GoM	**sw03_164a**	13/06/2003 09:47	-	11	Day + Night
GoM	**sw03_165a**	14/06/2003 16:06	-	11+1 part	Day + Night
GoM	**sw03_165b**	14/06/2003 13:38	-	17	Day + Night
GoM	**sw03_167a**	16/06/2003 15:26	-	2+1 part	Day
GoM	**sw03_173b**	22/06/2003 14:49	-	1	Night
Atlantic	**sw03_197a**	16/07/2003 10:44	-	2	Day
Atlantic	**sw03_197b**	16/07/2003 12:10	-	2	Day
Atlantic	**sw03_201b**	20/07/2003 15:15	-	2	Day
Atlantic	**sw03_202a**	21/07/2003 12:10	-	1	Day
Atlantic	**sw03_206a**	25/07/2003 11:59	-	4+1 part	Day
Atlantic	**sw03_206c**	25/07/2003 13:12	-	3	Day
Atlantic	**sw03_207a**	26/07/2003 11:28	-	4+1 part	Day
Mediterranean	**sw01_265**	21/09/2001 13:27	-	4	Day
Mediterranean	**sw01_275b**	01/10/2001 12:28	-	8+1 part	Day + Night
Mediterranean	**sw02_189b**	08/07/2002 18:16	-	1	Day
Mediterranean	**sw02_191b**	10/07/2002 09:01	-	5	Day
Mediterranean	**sw03_247a**	04/09/2003 17:14	-	4	Day + Night
Mediterranean	**sw03_249a**	06/09/2003 09:59	-	3	Day
Mediterranean	**sw03_249c**	06/09/2003 18:07	-	10+1 part	Day + Night
Mediterranean	**sw03_251a**	08/09/2003 08:25	-	8	Day
Mediterranean	**sw03_253a**	10/09/2003 09:29	-	7	Day
Mediterranean	**sw03_253b**	10/09/2003 09:38	-	18	Day + Night
Mediterranean	**sw03_253c**	10/09/2003 10:08	-	6+1 part	Day
Norway	**sw05_196a**	15/07/2005 14:43	Male	32	Day
Norway	**sw05_199a**	18/07/2005 13:05	Male	29	Day
Norway	**sw05_199b**	18/07/2005 14:43	Male	17	Day
Norway	**sw05_199c**	18/07/2005 16:57	Male	11	Day
Norway	**sw08_152a**	25/07/2003 11:59	Male	17	Day
Norway	**sw09_142a**	25/07/2003 13:12	Male	21	Day
Norway	**sw09_160a**	26/07/2003 11:28	Male	18	Day

2.2.2 Analysis of roll angles

The sperm whale is seen to have a very active rolling-behaviour when looking at the data from the Dtags. The overall occurrence of this rolling-behaviour does not seem to change with the depth of the dive. The whales seem to be changing their roll constantly, spinning fully around their own body axis or partially rolling from side to side.

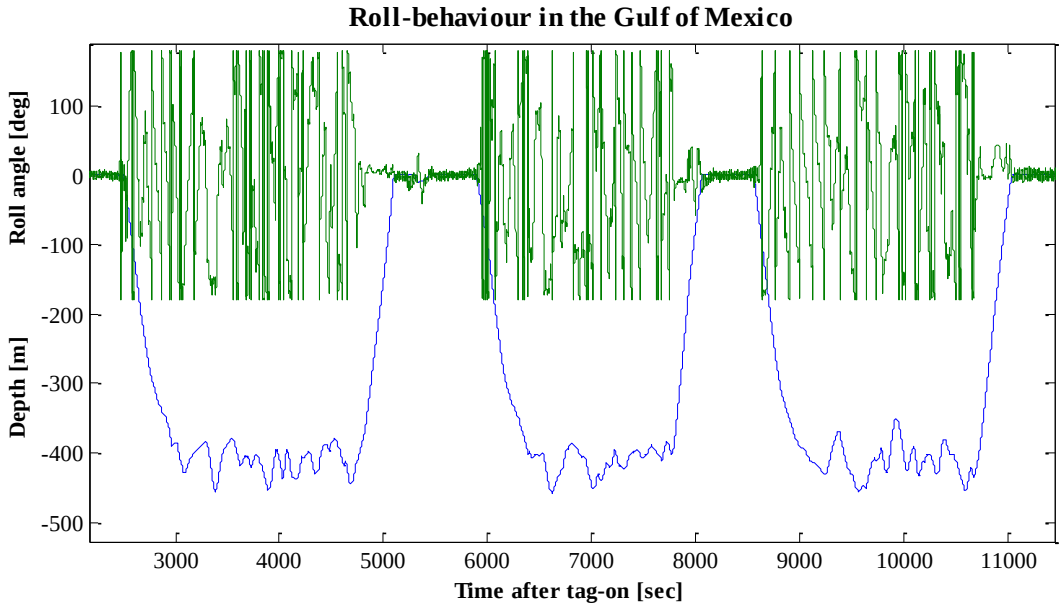

Figure 2.2 A typical dive profile from a sperm whale in the Gulf of Mexico (Sw01_200), showing three examples of dives and the roll-angles, illustrating the roll-behaviour in green above each of the dives. The time in seconds after the tag was attached to the whale is seen on the x-axis, and the dive depth in meters is shown on the lower part of the y-axis and the roll-angles from ± 180º on the upper part of the y-axis.

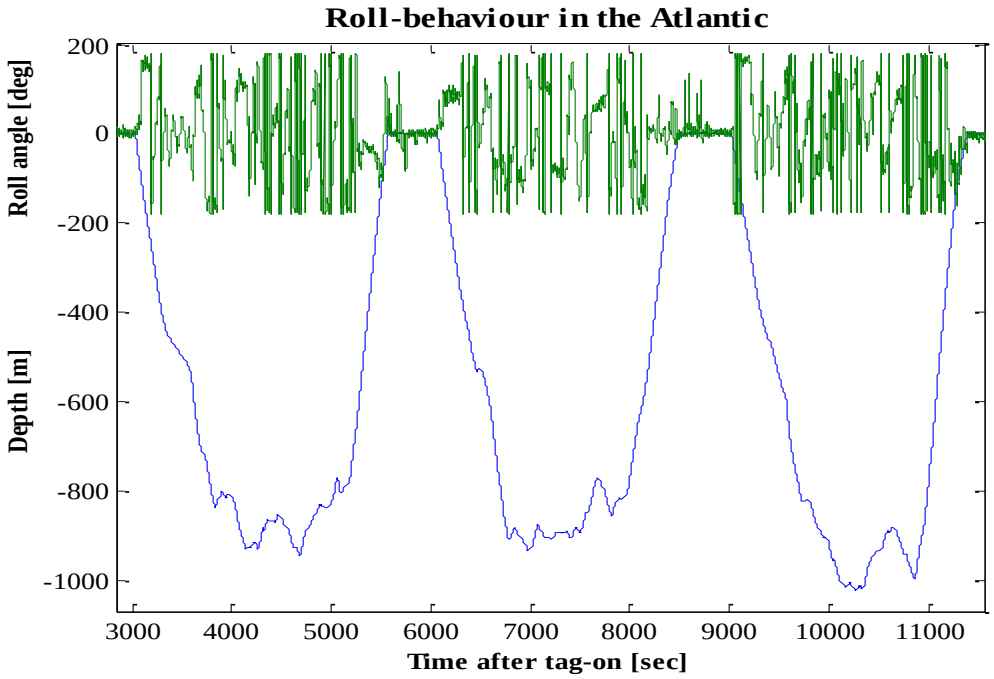

Figure 2.3 A typical dive profile from a sperm whale in the Atlantic (Sw03_206a), showing three examples of dives and the roll-angles, illustrating the roll-behaviour in green above each of the dives. The time in seconds after the tag was attached to the whale is seen on the x-axis, and the dive depth in meters is shown on the lower part of the y-axis and the roll-angles from ± 180º on the upper part of the y-axis.

Examining the relationship between pitch and roll during dives, distinct patterns seem to emerge from several whales. To look at all the data points for a full dive adds a great deal of clutter to the data of interest from when the whale is descending and ascending, as well as when the whale is at the surface. This will include a large number of data points at the negative pitch, when the whale is moving downwards as well as at the positive pitch when the whale swim towards the surface. To avoid this, all data points from the surface and down to 200 meter were eliminated and the remainder is plotted in the blue plot (Figure 2.4). Occasionally buzzes are produced while the whale is both descending and ascending, which is why the depth limit of 200 meters was chosen. As this study focuses on the foraging of these tagged whales and how they use roll for foraging, it would be interesting to examine if this tendency differs during the bottom interval when foraging is thought to be the most intense.

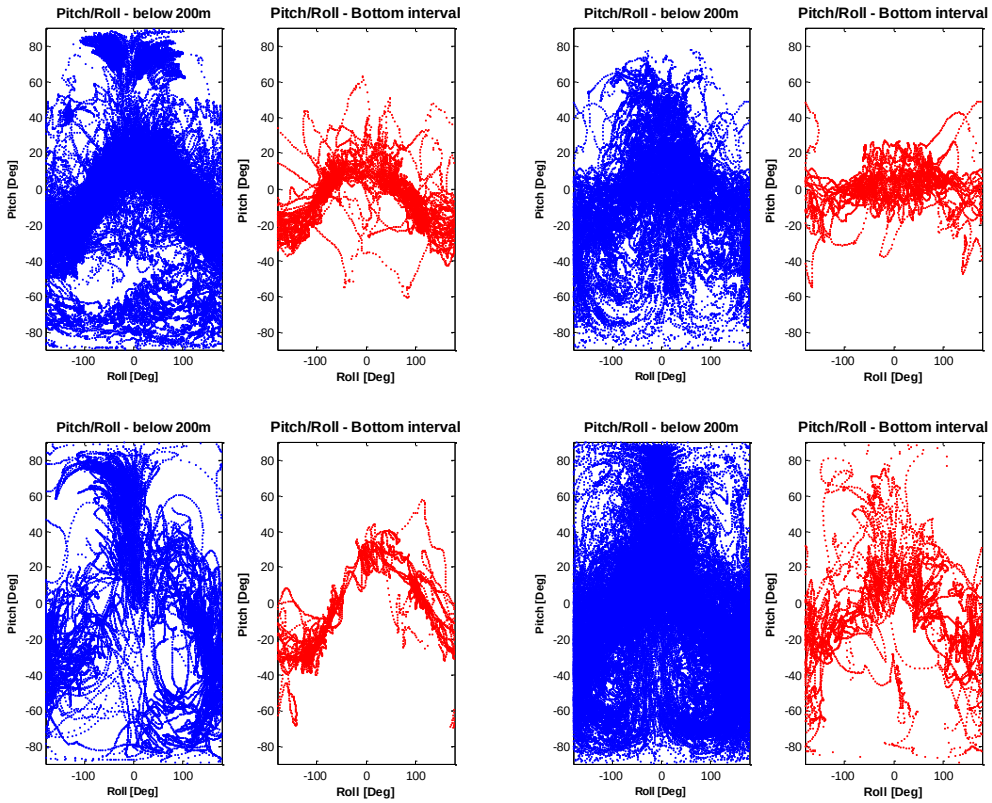

Figure 2.4 four examples of pitch/roll relationships illustrating a pattern found in a large number of the tagged whales at all four locations. (A) The blue plot represents the data points from one individual whale from all dives at depths deeper than 200 m. (B) The plot showing the red data points illustrates the data points collected from the bottom intervals collectively from all the dives from that particular individual.

In figure 2.4, the blue plot (A) illustrates the relationship between pitch and roll for all the dives for a single individual at depths deeper than 200 m including the bottom interval. In the red plot (B) this pitch/roll relationship are data points from the bottom interval alone, to see if there is a pattern emerging from this part of the dives separately.

The most frequent pattern observed when the pitch is negative (-90º to 0º), i.e. the whale is moving downwards, is that the whale has a tendency to be rolled either on its side, with either of its sides turned against the sea surface or upside-down with its ventral side against the sea surface (-90º to -180º or +90º to +180º). For positive pitch angles (0º to 90º) the whale seems to roll predominantly on the side or rightside-up with its dorsal side is turned towards the sea surface (-90º to +90º). A large number of whales from all four locations exhibited this pattern. Some show a strong pattern in the bottom interval alone, others in the general dives at depths deeper than 200 m as well. The strongest tendency shown is for the whales to be predominantly upside down at a high negative

pitch, others seem to be rolled upside down at an even lower negative pitch. The same pattern shows for the positive pitch, with some whales swimming upwards at a very steep pitch while being rolled rightside up, while others usually stay at a low positive pitch while swimming dorsal side up. A few whales show a very scattered pattern, not presenting any particular trend.

Clearly the roll of sperm whales is strongly related to their body pitch, so preferences in roll related to vision should control for the body pitch. To control for pitch, the whales' roll behaviour will be investigated during the bottom interval (defined in Miller et al., 2004) of each deep dive during each of three different pitch-modes: 1) when the whales pitch is at downward directed angles from -90 to -30 degrees, 2) when the whale is pitched around zero from -30 to 30 degrees and 3) when pitch is positive from 30 to 90 degrees and the whale is swimming upwards. At an upwards directed pitch, the whale has the opportunity to look straight ahead along its nose. This is another way for the whale to look towards the surface and in this pitch-mode, the whale is likely not limited by the roll angles. This advantage is not found for any of the other two pitch-modes, which are both limited by roll angles where the whale can look towards the surface.

Within each of the three pitch-modes (Downwards-directed, Flat and Upwards-directed pitch) the number of samples in the LURA is divided by the total number of samples in the pitch mode to obtain the proportion of time that roll falls within LURA.

In this study, the analyses are focussed on the bottom interval (illustrated in figure 2.5), because this is the part of the dive where the whale produces the most buzzes and are expected to be dedicating its time searching for, and attempting to capture, prey. The bottom interval is defined to begin "…when the pitch of the diving whale first exceeded 0º (when it was no longer oriented downwards). The start of the ascent was defined as the last point in time when an animal's pitch was downward (when it first pointed upward)." (Miller et al., 2004b).

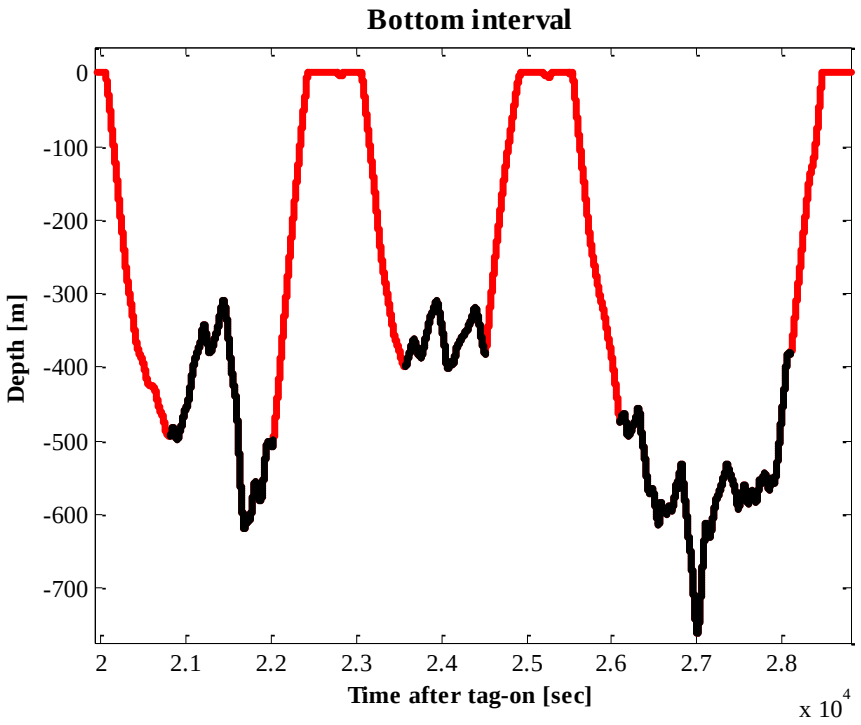

Figure 2.5 A typical dive profile where the depth of the whale is shown over time. The black line colour indicates the bottom interval, whereas the red line colour shows the remainder of the dive, descend, ascend and time spent at the surface.

For each of the tags, all dives are considered as separate dives and the order within the dive profile is not considered. Each bottom interval from individual dives has been divided into two phases: The Search-phase indicated by production of usual clicks, and the Buzz-phase indicating a prey capture attempt (Miller et al., 2004a). The search-phase is defined as the time during the bottom interval, excluding buzzes, focusing on the time before, after and in between the buzzes where the sperm whale is searching for prey. The buzz-phase is defined as the prey-capture attempts within the bottom-interval, from when the whale starts the fast repetition clicking locking on to the prey, and till the whale either stops the fast repetition clicking continuing straight into regular clicking or stop clicking followed by a pause. Each of these two phases is then separated into the three separate pitch modes, described earlier, giving a roll angle and a depth for each data point.

In both the Gulf of Mexico and the Mediterranean the recorded data contains dive profiles from both day and night time. When analyzing the effect of depth on roll angles

used by sperm whales at these two locations, separating the data into day and night dives gives the opportunity to look into a possible change in roll-behavior with depth, especially during the bottom interval, when there is available sunlight, and when there is not. If there is a change in roll-behavior based upon use of down-welling light by the foraging sperm whales, this change is expected to be reflected by how whales roll with respect to the LURA, the roll angles at which the whale would be able to benefit from the sunlight.

The buzz-phase was analysed separately to look for indications of vision use during the final stages of prey capture or the attempt to catch prey. Each of the samples within the buzz, records a roll angle and a depth, and a pitch angle by which the data record is separated into one of the three pitch-modes. The mean depth as well as a proportion of LURA is calculated for each pitch-mode. Buzzes are produced outside of the bottom interval as well, during the descent and ascent, which would result in the pitch being biased toward downwards directed or upwards directed pitch. Therefore only the buzzes produced during the bottom interval are considered in this study. This is the phase of the dive in which the whale's main purpose is expected to be to forage and the highest number of buzzes is produced (Miller et al., 2004b). An identical test as for the search-part data is performed for the buzzes, where the proportion of LURA is found for each of the three pitch-modes. This would then indicate a change in the whale's behaviour during day and night measurements. In the statistical analysis each buzz is expected to be independent, as the buzzes appear to be produced more or less at random, when the whale encounters a possible prey within depth-ranges of up to several hundred meters. Furthermore, the analysis is done on the proportion of roll and not the individual samples.

2.2.3 Statistics

The primary dependent variable in this study was the proportion of roll that falls within LURA to test if there is support for the hypothesis that sperm whales do indeed use their vision as a foraging strategy. Neither the proportion of roll falling within LURA nor the depths is normally distributed. Therefore a non-parametric Kruskal-Wallis test was chosen for the statistical analysis. The three pitch-modes were tested against each other

for each of the four locations, and in case of the null-hypothesis being rejected, a multicomparison test from the MatLab statistical Toolbox was used to test which one of the variables, either pitch-mode or location, were significantly different by comparing the rank means of the variables at a significance level of α=0.01.

The proportion of roll angles within LURA for each of the individual dives is expected to be independent. Furthermore the separate dives are considered independent from each other because of the 3D environment the sperm whales live in. Even though depth might be the same between two dives, the change in environment could be relatively large, such as in- or outside a canyon, or a change in seabed contour. Though sperm whales are thought to exhibit behaviour patterns independently from one dive to the next, it is possible that conditions change slowly so that they are not truly independent. In the case of the data not being independent, the p-values would show up as lower values than they would have been otherwise. Therefore, to be conservative to this possible effect, the p-level for statistical significance was set to α=0.01 in this study, instead of the usual α =0.05.

2.3 Results

For the analysis, the bottom interval has been separated into the search-phase and buzz-phase. The number of dives with the search-phase during the bottom-interval and the number of buzzes used for the analysis is summarised in Table 2.2.

Table 2.2 an overview the number of dives and buzzes used in the analysis for each of the four locations. A partial dive is defined as a dive that does not have an ascent-phase because of the tag releasing from the whale in the middle of the dive.

Location	**Number of full dives**	**Number of partial dives**	**Number of buzzes - day**	**Number of buzzes - night**
Gulf of Mexico	134	10	1481	879
North Atlantic	18	2	308	-
Mediterranean	74	1	662	74
Norway	145	0	735	-

2.3.1 Search phase

In general the proportions of roll falling within LURA are distributed around the 0.75 proportion that would be expected for a random distribution of roll angles. Looking within the three pitch modes for each of the four locations, three of these locations (Figure 2.6: **A** - Gulf of Mexico, **B** - Mediterranean and **D** - Norway) show a higher number of dives in which the whales spend more time at angles where they are predicted to be able to see toward the sea surface, except for **C** (Atlantic) where the number of dives are more focussed around a roll proportion just around the 0.75 line.

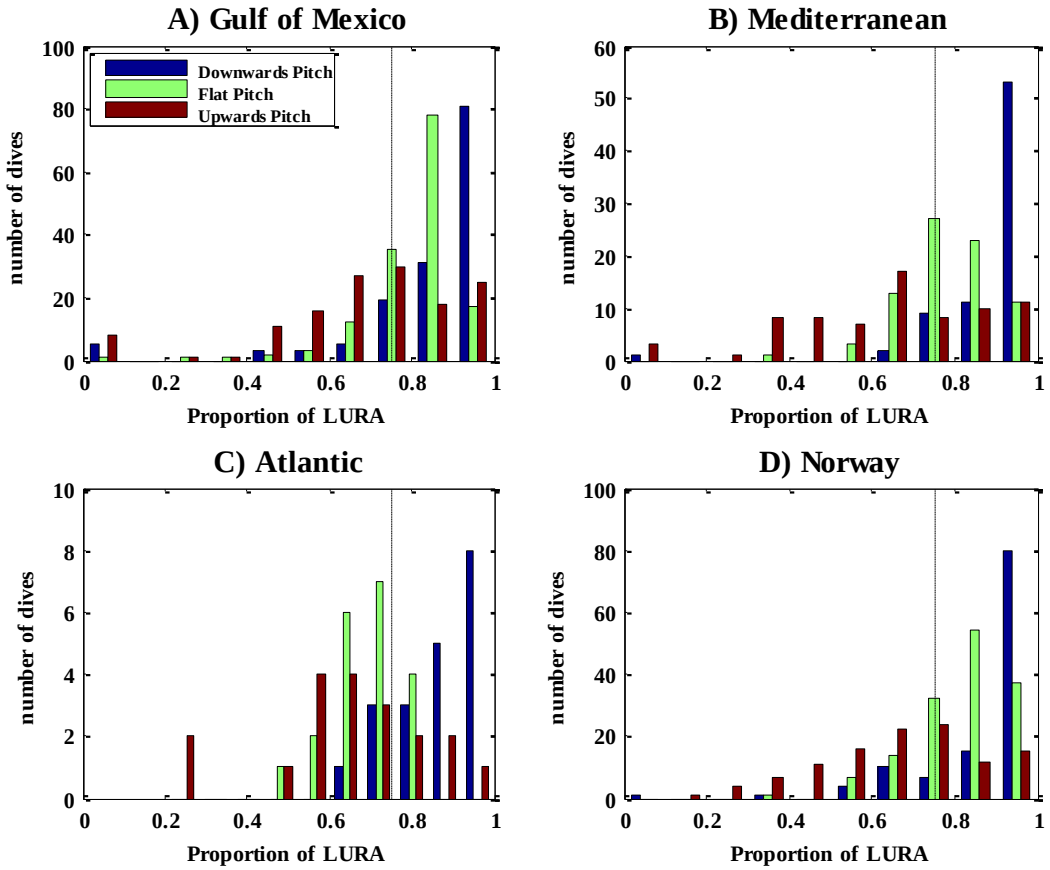

Figure 2.6 Histogram of the proportion of roll angles falling within LURA by sperm whales while searching during the bottom interval of dives. A separate histogram is given for each of the three pitch modes for each location. All of the data from each location is shown so A) and B) represents combined day and night time data and C) and D) are only day time data. The x-axis shows the proportion of roll falling within LURA, and the Y-axis shows the number of dives. Blue bars show data during downwards directed pitch (-90° to -30°) modes, green bars data during flat pitch (-30° to 30°) and data during upwards directed pitch (30° to 90°) is shown as red bars. The proportions of roll falling within

LURA on the x-axis represents the proportion of time that the whale is rolled at angles where it should be able to see upwards toward the lighter sea surface (see figure 2.1).

Looking at the difference between the proportion of roll for the pitch-modes in the Gulf of Mexico (**A**) a Kruskal-Wallis test does show that even though the proportion of roll that falls within LURA is above the 0.75 line for both the flat and the downwards directed pitch, the proportion is significantly higher when the whale is at a downwards directed pitch than in the other two pitch modes (Kruskal-Wallis Chi^2=76.12 p=0; n_{Down}=147, n_{Flat}=150 and n_{Up}=137). The same pattern is apparent for the Mediterranean (**B**) as well with the proportion of roll being higher for both downwards directed and flat pitch, the proportion of LURA is still significantly higher when the whale is swimming downwards compared to the other two pitch-modes (Kruskal-Wallis Chi^2=71.09 p=$3.33*10^{-16}$; n_{Down}=76, n_{Flat}=78 and n_{Up}=73).

For the third location, the Atlantic (**C**) the proportion of roll that falls within LURA shows a lower overall tendency compared to the other locations, especially for the flat pitch-mode, which usually has a generally high proportion of LURA. Here the proportion of roll that is within LURA is definitely higher in the downwards directed pitch-mode, which is supported by the statistic (Kruskal-Wallis Chi^2=22.03 p=$1.64*10^{-5}$; n_{Down}=20, n_{Flat}=20 and n_{Up}=19). The last location is northern Norway (**D**) in which a higher number of dives have a high proportion of roll within LURA for the flat pitch mode and which again seems to be centred above the 0.75 line. This is the same tendency as seen for the downwards directed pitch, where the upwards directed pitch is centred at a lower proportion of LURA, around the 0.75 line. The statistics also show this pattern, where the upwards directed pitch is shown to be statistically different from the other two pitch-modes (Kruskal-Wallis Chi^2=97.94 p=0; n_{Down}=118, n_{Flat}=118 and n_{Up}=112). Thus, for all locations, the proportion of roll within LURA was highest during downward motion, when pitch was less than -30°.

When comparing the overall proportion of roll angles that fall within LURA across the four locations, the tagged whales in the Atlantic spent less time at angles where they are assumed to be able to look upwards towards the downwelling light than the other three locations (Kruskal-Wallis Chi^2=23.24 p=$3,59*10^{-5}$; n_{GoM}=291, $n_{Atlantic}$=59, n_{Med}=163 and n_{Norway}=348).

2.3.2 Buzz phase

How were the tagged whales oriented while capturing the prey during the buzz? Did they show the same tendency as seen during the search-phase, or did they show a very different roll-behaviour?

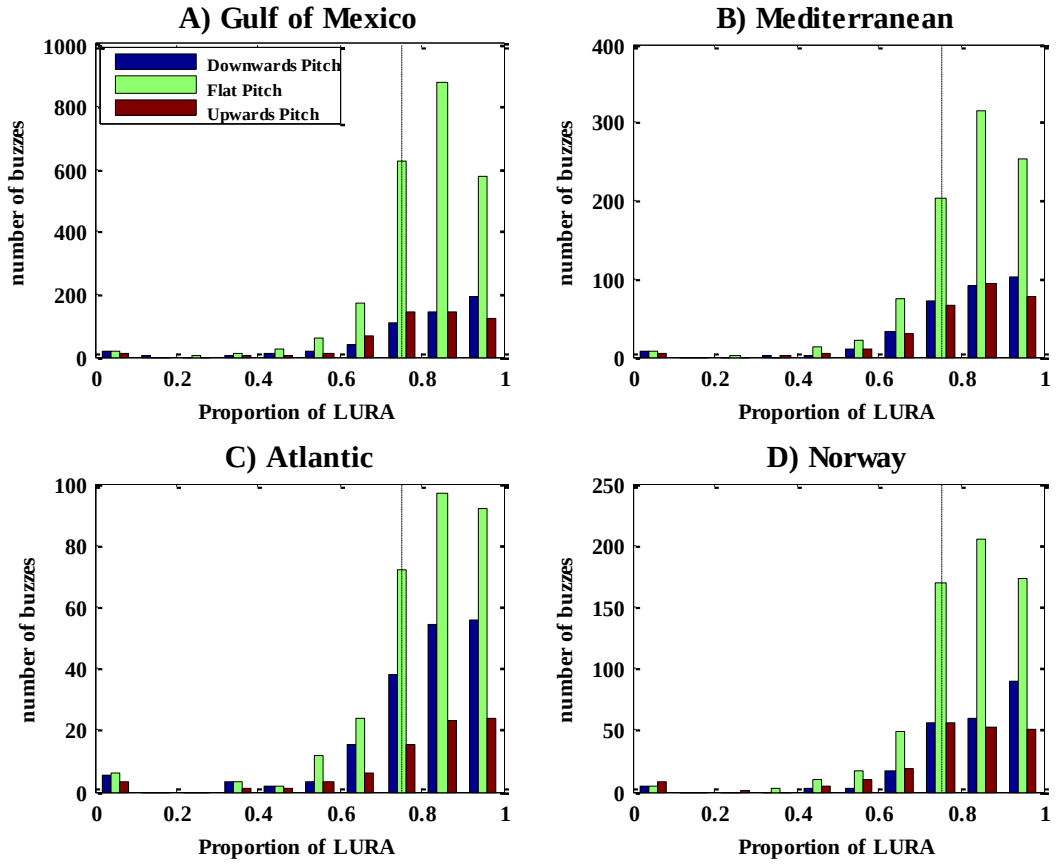

Figure 2.7 Histogram of LURA roll angles employed by sperm whales during buzzes within the bottom interval of dives. A separate histogram is given for each of the three pitch modes for each location. Each plot shows a separate histogram for each of the three pitch modes for each location during the buzz phase. A) and B) are combined day and night time data and C) and D) are only day time data. The x-axis shows the proportion of roll that fell within LURA, and the y-axis shows the number of dives with the appropriate roll values. Blue bars show data during downwards directed pitch (-90° to -30°), green bars show data during flat pitch (-30° to 30°) and the data during upwards directed pitch (30° to 90°) is shown as red bars. The proportions of roll angles within LURA on the x-axis represents the proportion of time that the whale is rolled at angles where it should be able to see upward toward the lighter sea surface (see figure 2.4).

There was little variation in the proportion of roll within LURA across all of the locations (Figure 2.7: A, B, C and D) and across the three different pitch bins, with most data points close to the 0.75 proportion line or above it. To test if there was a difference between the four locations, the overall roll proportion was tested using a Kruskal-Wallis nonparametric test. The test resulted in a p-value that showed no significant difference in roll proportion between the four locations (Kruskal Wallis: chi^2=7.19 and p=0.0661; n_{GoM}=2146, $n_{Atlantic}$=560, n_{Med}=1094 and n_{Norway}=1056). To go into more detail and look at each of the pitch-modes at these four locations, it is seen that the majority of the buzzes were produced while the whale is at a relatively flat pitch during the bottom phase. This tendency is seen for all locations regardless of the number of buzzes produced. The buzzes produced at a pitch that is either downward or upwards directed seems fairly equal for three of the locations: the Gulf of Mexico (**A**), the Mediterranean (**B**), and Norway (**D**). But in the Atlantic (**C**) the whales seem to be at a downward directed pitch more frequently when buzzing than at an upright directed pitch.

The tagged whales in the Gulf of Mexico seem to be spending more time at angles where they can look upwards when buzzing at a flat pitch compared to the roll proportions for the other two pitch bins, which are all concentrated in the high end of the proportions for LURA. When tested, the proportion of roll falling within LURA during the downwards directed pitch have been found to be significantly different from the proportion of roll falling within LURA when the whale is swimming at an upwards directed pitch (Kruskall-Wallis Chi^2=20.11 p=3.4*10^{-5}; n_{Down}=524, n_{Flat}=2360 and n_{Up}=507). In the Mediterranean the proportion of roll within LURA did not differ across the three pitch-modes (Kruskall-Wallis Chi^2=2.46 p=0.2928; n_{Down}=318, n_{Flat}=887 and n_{Up}=285). The distribution of buzzes in the Atlantic seems different from the other three locations, due to the fact that the number of buzzes produced while the whale is at a downwards directed pitch is considerably higher than for the upwards going pitch, which is different from the other locations, where they are almost the same. But tests have shown that the mean proportion of LURA for each of the pitch-modes are not significantly different from each other in the Atlantic data (Kruskall-Wallis Chi^2=0.83 p=0.6589; n_{Down}=176, n_{Flat}=308 and n_{Up}=76). Once again, flat pitch is the dominating pitch-mode during buzzes produced in northern Norway (**D**). And as seen at two of the

three other locations, the downwards and upwards directed pitch is almost equal in number of buzzes produced, though with a slightly higher number of buzzes when the whales are at angles where they can see towards the surface. Tests show that the amount of roll falling within LURA within the upwards directed pitch are significantly lower than the downwards directed pitch (Kruskall-Wallis Chi^2=18.77 $p=8.36*10^{-5}$; n_{Down}=231, n_{Flat}=626 and n_{Up}=199).

2.3.3 Day versus night

At two locations, the Gulf of Mexico and the Mediterranean, the Dtag was attached to 11 and 4 whales, respectively, making it possible to compare the proportion of roll-angles within LURA to see if there was a difference in the roll-behaviour during the day compared to the night time.

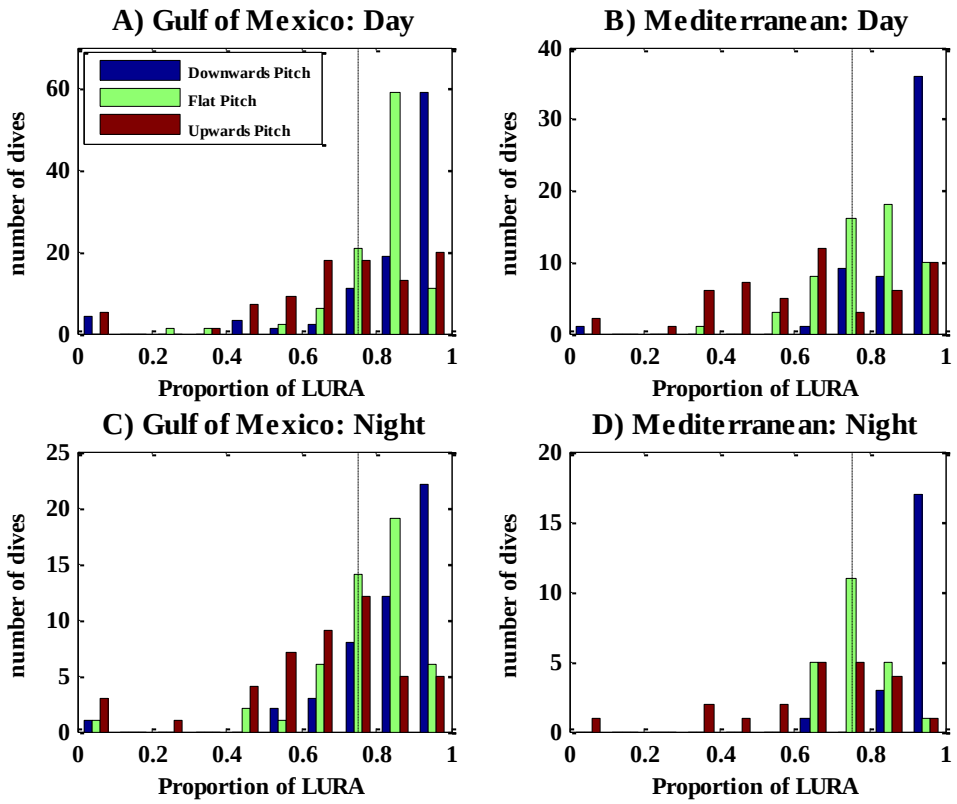

Figure 2.8 Histogram of LURA roll angles employed by sperm whales during the search-phase within the bottom interval of dives. A separate histogram is given for each of the three pitch modes for each location.

Each plot shows a separate histogram for each of the three pitch modes for each location during the search phase. A) is day time data from the Gulf of Mexico and B) is day time data from the Mediterranean and C) is night time data from the Gulf of Mexico and D) is night time data from the Mediterranean. The x-axis shows the proportion of roll that fell within LURA, and the y-axis shows the number of dives with the appropriate roll values. Blue bars show data during downwards directed pitch (-90° to -30°), green bars show data during flat pitch (-30° to 30°) and the data during upwards directed pitch (30° to 90°) is shown as red bars. The proportions of LURA on the x-axis represents the proportion of time that the whale is rolled at angles within LURA and it should be able to see upward toward the lighter sea surface (see figure 2.4).

Looking at the difference between the proportion of roll for the pitch-modes during the day in the Gulf of Mexico (**A**) a Kruskal-Wallis test does show that the proportion of LURA is significantly higher when the whale is at a downwards directed pitch (Kruskal-Wallis Chi^2=46.72 $p=7.17*10^{-11}$; n_{Down}=99, n_{Flat}=101 and n_{Up}=91). The same pattern is apparent for the Mediterranean (**B**) as well with the proportion of roll being significantly higher when the whale is swimming downwards compared to the other two pitch-modes (Kruskal-Wallis Chi^2=41.1 $p=1.19*10^{-9}$; n_{Down}=55, n_{Flat}=56 and n_{Up}=52).

For the night time in the Gulf of Mexico, the whales show a significant lower proportion of LURA when swimming at an upwards directed pitch compared to the flat and downwards directed pitch-mode (Kruskal-Wallis Chi^2=31.42 $p=1.51*10^{-7}$; n_{Down}=48, n_{Flat}=49 and n_{Up}=46). In the Mediterranean the general proportion of roll is above 0.5 and centred just around the 0.75 mark, though with a higher number of dives with high proportion of LURA when swimming downwards, which shows to be significantly different from the proportion of roll for the other two pitch-modes (Kruskal-Wallis Chi^2=31.03 $p=1.82*10^{-7}$; n_{Down}=21, n_{Flat}=22 and n_{Up}=21). Comparing the two locations at night did not show any significant differences (Kruskal-Wallis Chi^2=0.1 p=0.7515; n_{GoM}=101 and n_{Med}=91).

The difference in the overall distribution of roll proportion falling within LURA for day and night within each location is not great, and when testing the difference statistically it showed no significant difference for either the Gulf of Mexico or the Mediterranean (Kruskal-Wallis Chi^2=3.83 p=0.503; n_{Day}=291 and n_{Night}=243 and Kruskal-Wallis Chi^2=0.16 p=0.6847; n_{Day}=163 and n_{Night}=64, respectively).

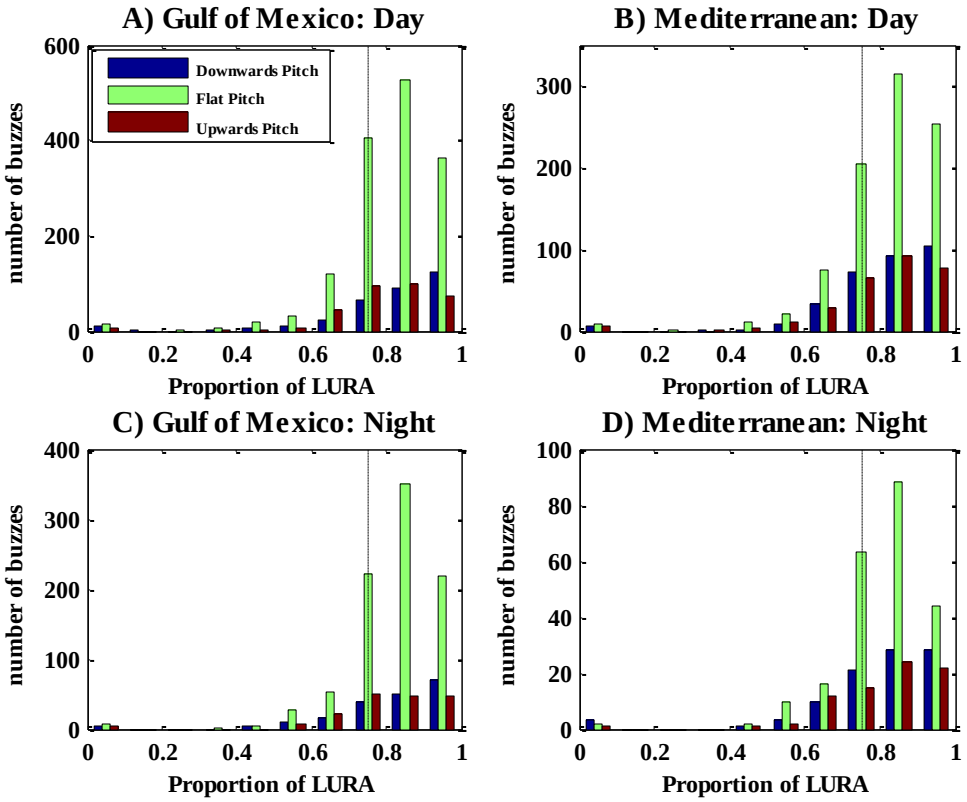

Figure 2.9 Histogram of LURA roll angles employed by sperm whales during buzzes within the bottom interval of dives. A separate histogram is given for each of the three pitch modes for each location. Each plot shows a separate histogram for each of the three pitch modes for each location during the buzz phase. A) is day time data from the Gulf of Mexico and B) is day time data from the Mediterranean and C) is night time data from the Gulf of Mexico and D) is night time data from the Mediterranean. The x-axis shows the proportion of roll that fell within LURA, and the y-axis shows the number of dives with the appropriate roll values. Blue bars show data during downwards directed pitch (-90° to -30°), green bars show data during flat pitch (-30° to 30°) and the data during upwards directed pitch (30° to 90°) is shown as red bars. The proportions of roll angles within LURA on the x-axis represents the proportion of time that the whale is rolled at angles where it should be able to see upward toward the lighter sea surface (see figure 2.4).

The tagged whales in the Gulf of Mexico seem to be spending more time at angles where they can look upwards when buzzing at a flat pitch compared to the roll proportions for the other two pitch bins, which are all concentrated in the high end of the proportions for LURA. When tested, the proportion of roll falling within LURA during the downwards directed pitch have been found to be significantly different from the proportion of roll when the whale is swimming at an upwards directed pitch (Kruskall-

Wallis Chi^2=18.11 p=0.0001; n_{Down}=332, n_{Flat}=1481 and n_{Up}=333). In the Mediterranean the data shows the same tendency with proportion of LURA during flat pitch being at a higher frequency than the other two pitch-modes, but this did not show in the statistical tests for the three pitch-modes (Kruskall-Wallis Chi^2=3.42 p=0.1806; n_{Down}=224, n_{Flat}=662 and n_{Up}=208).

The Night time data shows a very similar distribution of roll proportions (Figure 2.9: **E** and **F**). The two locations: the Gulf of Mexico (**E**) and the Mediterranean (**F**) both show the same tendency to have a general high proportion of LURA, as seen during the day as well. Again the two locations were compared to see if there was an overall difference in the roll proportion between the two. The result showed no significant difference in the proportion of LURA between the two locations at night (Kruskall-Wallis Chi^2=2.94 p=0.0867; n_{GoM}=1245 and n_{Med}=396). Looking at the individual pitch-modes, it is clear that the flat pitch is still dominating in numbers for both locations. For the Gulf of Mexico the tests showed no significant differences in the mean roll proportion for the three pitch-modes (Kruskall-Wallis Chi^2=3.32 p=0.1898; n_{Down}=192, n_{Flat}=879 and n_{Up}=174). When comparing the pitch-modes for the Mediterranean it shows a resembling result, though with a smaller number of buzzes, i.e., that the tagged whales do not spend significantly more time at angles where they can look upwards at any pitch-mode at night (Kruskall-Wallis Chi^2=0.29 p=0.8651; n_{Down}=94, n_{Flat}=25 and n_{Up}=77).

The difference in the distribution of roll proportions at night versus the day is very similar, and when tested for each of the two locations where data was available for both day and night, the Gulf of Mexico and the Mediterranean, they both had similar results. As shown in both the day and night plots the distribution of roll proportion for each of the daytime buzzes and buzzes produced at night is not significantly different which was found with a nonparametric Kruskal-Wallis test as well for both the Gulf of Mexico and the Mediterranean (Kruskall-Wallis **GoM:** Chi^2=2.43 p=0.1192; n_{Day}=2146 and n_{Night}=1245, and **Mediterranean:** Chi^2=5.93 p=0.0149; n_{Day}=1094 and n_{Night}=396).

2.3.4 Difference by depth during day and night

Foraging was observed at various depths for each of the four locations analyzed. As described in Watwood et al. (2006), the tagged whales were found to dive deeper in the Atlantic compared to the Mediterranean and the Gulf of Mexico. The whales tagged in northern Norway have a very different dive pattern. They are found to be foraging at both shallow depths as well as similar deeper depths observed at the remaining three locations (Teloni et al., 2008). This can be seen by the separation of data point clusters (magenta for Norway) in figures 2.6-2.15.

2.3.4.1 Search-phase: Downwards directed pitch

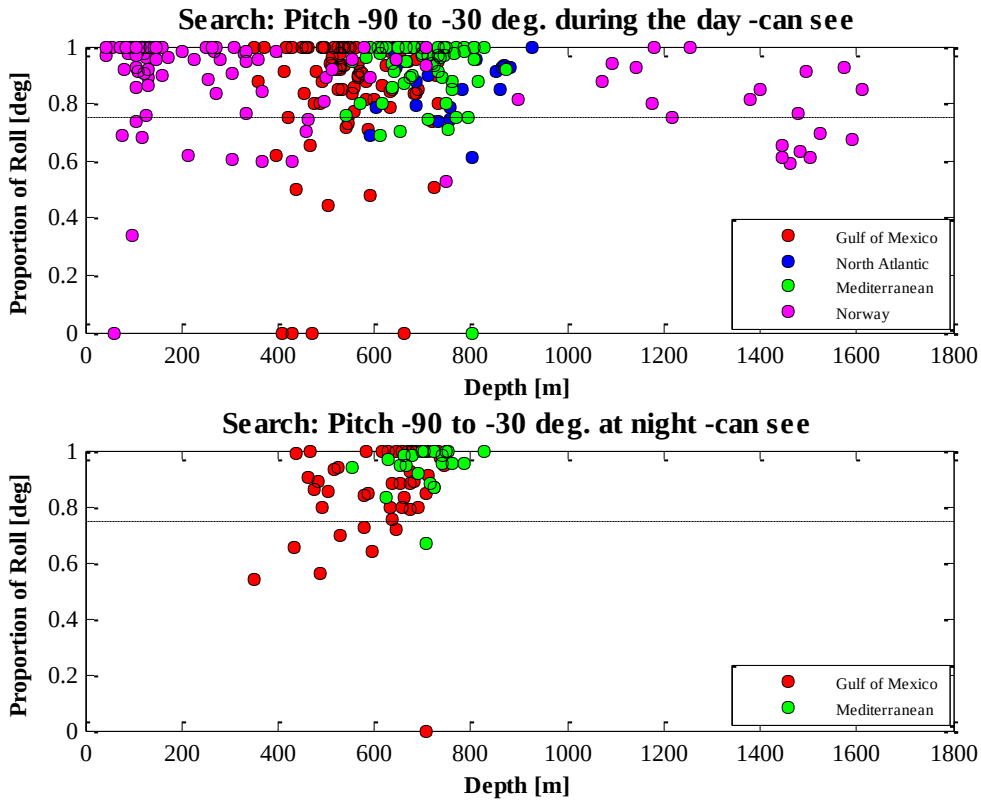

Figure 2.10 The proportion of roll within LURA is illustrated as a function of the mean depth for each dive in the downwards directed pitch mode. This figure shows data during the downwards directed pitch mode during the searching part of the bottom interval. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf

of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

When the whale has made a decision to level out and focus on foraging in the bottom interval of its dive, it still maneuvers in all directions, changes its pitch and is constantly rolling presumably to search an area or to close up on a possible prey. Looking at the part of the foraging interval where the whale is searching for prey at a downwards directed pitch in Figure 6, the roll proportion and depth for each dive is marked by a dot. During the day the distribution of dots for each of the locations concentrated in clusters above the 0.75 proportion line with a few outliers at or below it. If a dot is positioned at either one or zero it means that the whale spends either all the time at roll angles where it is able to see the sea surface or that it spends no time at the angles looking upwards, respectively. At deeper depths the dots representing the northern Norway data set, are distributed further apart from each other around the 0.75 line. At night, the proportion of roll angles that fall within LURA resembles the proportion of angles within LURA at both locations, compared to the day time. This indicates that when they are pitched downwards, sperm whales appears to roll at angles where they are able to look towards the surface with no difference between the day and night time (Kruskall-Wallis **GoM:** $Chi^2=1.3$ $p=0.2545$; $n_{Day}=99$ and $n_{Night}=48$, and **Mediterranean:** $Chi^2=0.84$ $p=0.359$; $n_{Day}=55$ and $n_{Night}=21$).

2.3.4.2 Search-phase: Flat pitch

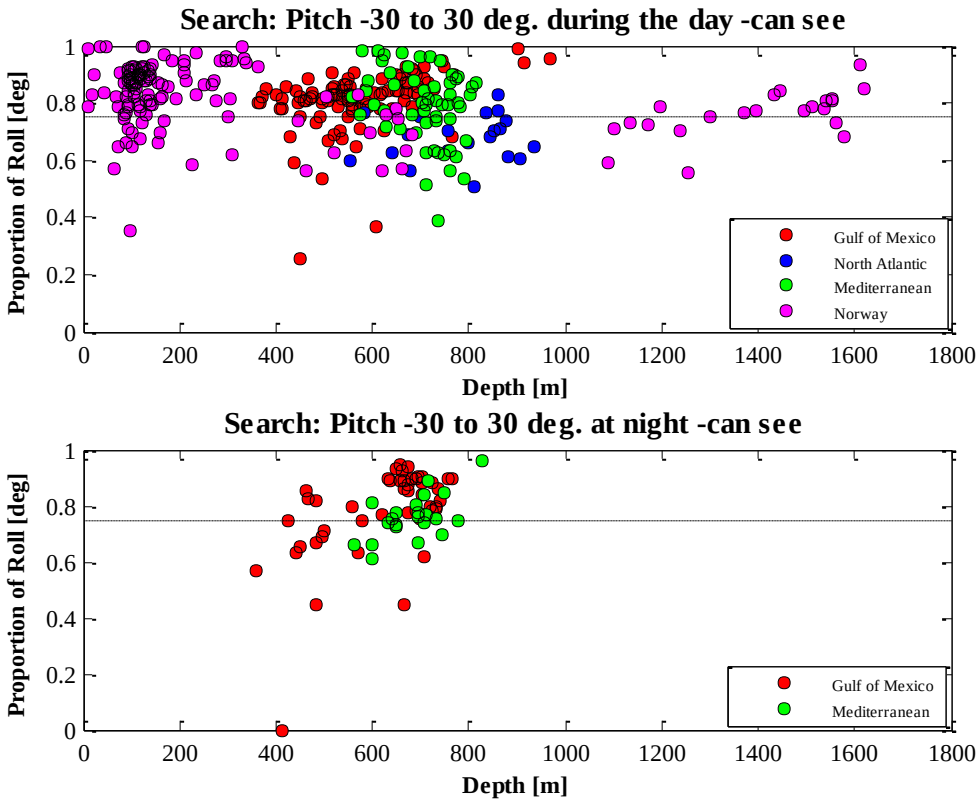

Figure 2.11 The proportion of roll within LURA is illustrated as a function of the mean depth for each dive in the flat pitch mode. This figure shows data during the flat pitch mode during the searching part of the bottom interval. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

In the flat pitch-bin the data analyzed is from the tagged whales found at a pitch between -30 to 30 degrees while they are searching for prey during the bottom interval (figure 2.11). During the day, the data set from the Gulf of Mexico is predominately clustered above the 0.75 line with a few outliers at or below the line. The same tendency is seen for the data from the Mediterranean where the Atlantic shows a different, less tight distribution mainly at and below the 0.75 line. The proportion of roll angles within LURA does not seem to change strongly with depth at these three locations, except for three outliers from the Gulf of Mexico at a deeper depth than the rest of the dives, all

close to the 0.9-1.0 proportion of roll, meaning that here, the whales have been at an angle where they are able to look upwards for most of the time at a flat pitch. The mean depths for the northern Norway data set are once again separated at a cluster at a shallower depth where the cluster is centered above the 0.75 line, where the deeper depths show a less tight distribution just above and below the line. At night the data from the Gulf of Mexico shows a minor separation where the proportion of LURA is distributed above the 0.75 line and the remainder of the data is centered just below the line. For the Mediterranean, the data set does not show any specific change in roll proportion in the day versus night (Kruskall-Wallis **GoM:** Chi^2=0.3036 p=0.5816; n_{Day}=101 and n_{Night}=49, and **Mediterranean:** Chi^2=2.7 p=0.1003; n_{Day}=56 and n_{Night}=22). This indicates that the whales are rolled upside down and on the side for the majority while searching in the bottom-interval with no regards to the time of day.

2.3.4.3 Search-phase: Upwards directed pitch

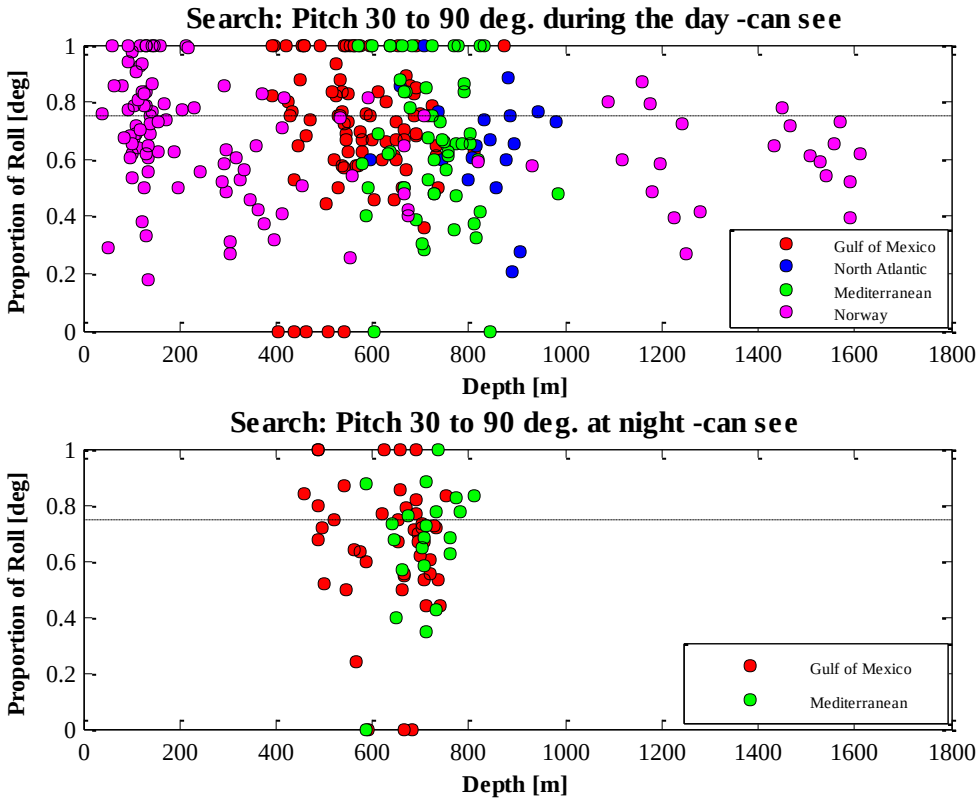

Figure 2.12 The proportion of roll within LURA is illustrated as a function of the mean depth for each dive in the upwards directed pitch mode. This figure shows data during the upwards directed pitch mode during the searching part of the bottom interval. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

When looking at the search part of the bottom interval when the whale is at an upwards directed pitch, the Gulf of Mexico dives show a different pattern than seen in the other two pitch-modes. The data points are scattered, and centered just below the 0.75 line, showing that the whales are rolled at angles outside the LURA for longer than expected by chance during the day with no apparent effect by increasing depth. This also seems to be the case for both the Atlantic and the Mediterranean, whereas the dives from northern Norway show a separation in both depth and proportion of LURA. The shallow dives are centered at the 0.75 line whereas the remainder of the dives is predominantly below the line, showing a proportion of LURA less than expected by chance. Dives performed during the night, with no sunlight available shows, as seen during the day, a proportion of roll centered at a roll proportion a little below what is expected by chance for the dives from both locations (Kruskall-Wallis **GoM:** Chi^2=2.96 p=0.0892; n_{Day}=91 and n_{Night}=46 and **Mediterranean:** Chi^2=0.16 p=0.6915; n_{Day}=52 and n_{Night}=21), showing no difference in daytime and night time roll-behaviour. This means that when the whales are pitched at an upwards directed pitch, they have a tendency to be rolled at more omnidirectional angles than seen for the other two pitch-modes, showing no difference in night and day.

2.3.4.4 Buzz-phase: Downwards directed pitch

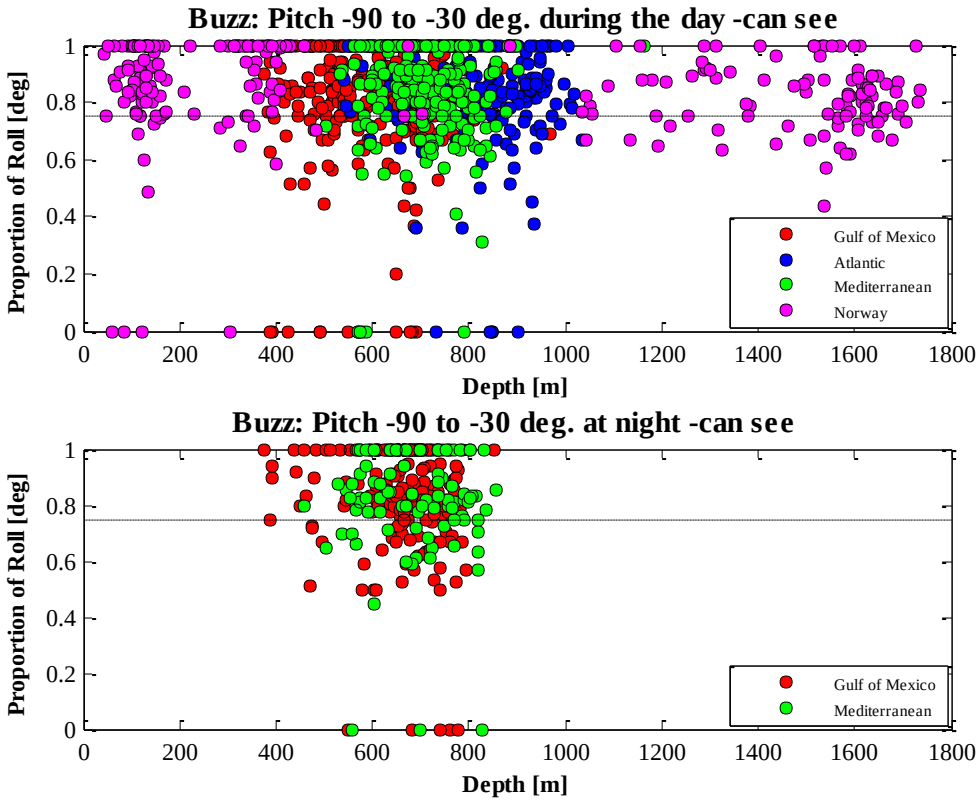

Figure 2.13 The proportion of roll within LURA is illustrated as a function of the mean depth for each buzz in the downwards directed pitch mode. This figure shows data during the downwards directed pitch mode during the buzzes in the bottom interval. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

When the whale is buzzing the whale is presumed to have found a prey-item and locked onto it with its echolocation. Figure 2.13 illustrates the proportion of roll falling within LURA during the buzz-phase within each of the four locations when the whale is at a downwards directed pitch and within the bottom interval of each dive. The distribution for three of the locations, the Gulf of Mexico, the Atlantic and the Mediterranean are all clustered around the 0.75 line, with the majority of data points above it, not showing any specific changes in mean depth for any of them, neither of them indicating an influence

by depth. The depth separation in the data points for northern Norway is divided into roughly three parts, where the two shallower ones are tightly clustered above and around the 0.75 line, and the portion of data points at deeper mean depths, where no light is available, show proportions of roll falling within LURA to be centered at the 0.75 line and just above it. At night, where no light is available as well at any depth, the distribution of data points is centered on the 0.75 line, with no apparent change in depth. There was no difference between day and night time, within each of the two locations, the Gulf of Mexico and the Mediterranean (Kruskall-Wallis **GoM:** Chi^2=0.26 p=0.6080; n_{Day}=332 and n_{Night}=192, and **Mediterranean:** Chi^2=0.3 p=0.5844; n_{Day}=224 and n_{Night}=94).

2.3.4.5 Buzz-phase: Flat pitch

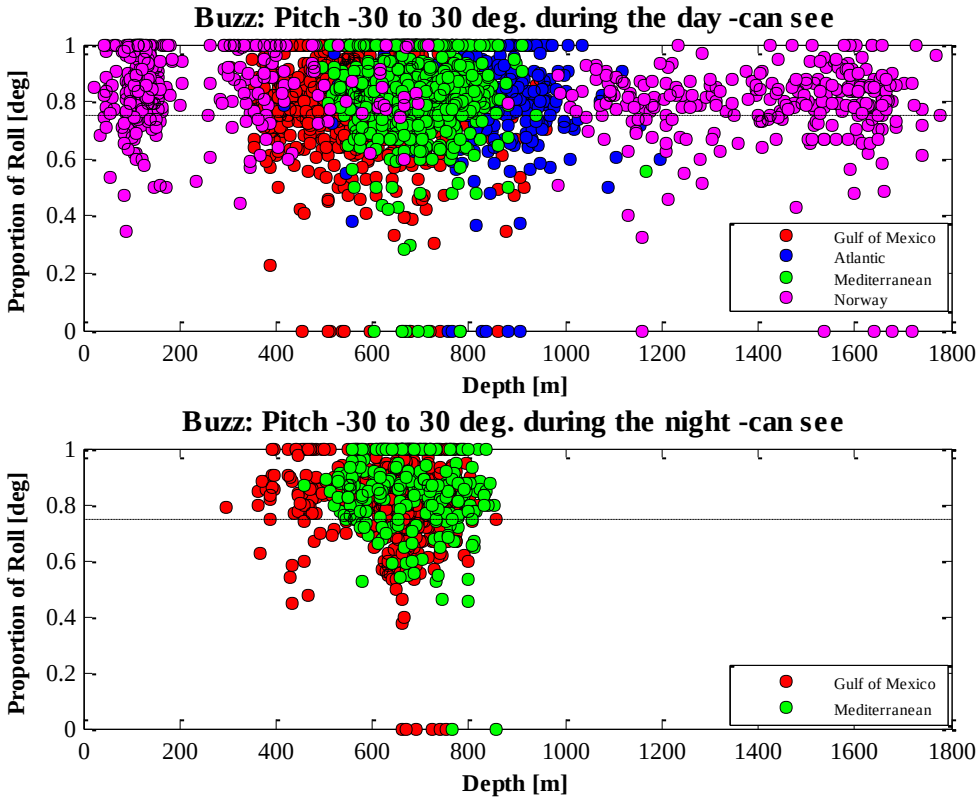

Figure2.14 The proportion of roll within LURA is illustrated as a function of the mean depth for each buzz in the flat pitch mode. This figure shows data during the flat pitch mode during the buzzes in the bottom phase. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the

Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

For the buzzes produced at a flat pitch, the depth distribution for each of the four locations does not seem to change. The proportion of roll falling within LURA for each of the three locations the Gulf of Mexico, the Atlantic and the Mediterranean are also very similar and all tightly clustered around the 0.75 line. The data from northern Norway shows the same overall distribution of proportions of LURA, but centered slightly above the 0.75 line for all depths. At night both locations show a tight cluster at the same depths with the majority of proportion of LURA above the 0.75 line. A part of the buzzes from the Gulf of Mexico is produced at a shallower depth and predominantly with a higher proportion than the 0.75 expected by chance, but without showing any difference between the day and night data when the whales are buzzing at a flat pitch in the Gulf of Mexico (Kruskall-Wallis **GoM:** $Chi^2=2.66$ $p=0.1027$; $n_{Day}=1481$ and $n_{Night}=879$, and **Mediterranean:** $Chi^2=7.26$ $p=0.0071$; $n_{Day}=662$ and $n_{Night}=225$). The proportion of angles within LURA was found to be significantly higher during the day in the Mediterranean compared to the night time, though with the majority of roll-proportions seen at night appearing to be well above what was expected by chance.

2.3.4.6 Buzz-phase: Upwards directed pitch

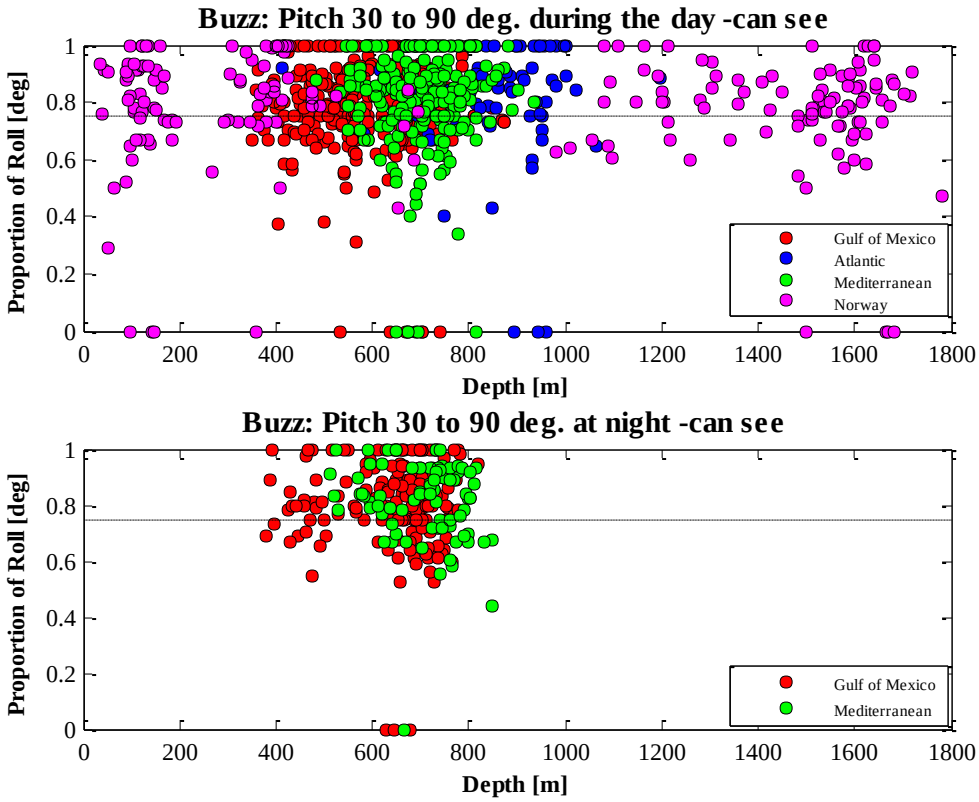

Figure 2.15 The proportion of roll within LURA is illustrated as a function of the mean depth for each buzz in the upwards directed pitch mode. This figure shows data during the upwards directed pitch mode during the buzzes in the bottom interval. The day-time dataset which consists of data from four locations: the Gulf of Mexico (red), the Mediterranean (blue), the Atlantic (green) and northern Norway (magenta) is shown in the top plot. The bottom plot shows the night time dives for two locations, the Gulf of Mexico (red) and the Mediterranean (blue). The dashed black line indicates the 0.75 proportion of roll expected by chance to fall within LURA.

When the whales pitch was upwards directed and the whale was buzzing, the data shows that in the Gulf of Mexico the buzzes are produced while the whale is mainly rolled at angles where it is able to see the surface for a greater proportion of time than expected by chance. The same pattern is showing for the Mediterranean, whereas the buzzes produced in the Atlantic are produced with a proportion of LURA predominantly above the 0.75 line, though with a few outliers below the proportion expected by chance. For northern Norway, the proportion of LURA does not change mentionable with depth, with the

majority of roll proportions centred a little above the 0.75 line. During the night, the buzzes produced in the Gulf of Mexico are once again located just around the 0.75 line for all depths, which seems to be the case for the buzzes produced in the Mediterranean as well (Kruskall-Wallis **GoM:** Chi^2=1.05 p=0.3048; n_{Day}=333 and n_{Night}=174, and **Mediterranean:** Chi^2=0.06 p=0.7991; n_{Day}=208 and n_{Night}=77). This result indicates that no difference in proportion of angles within LURA was found for buzzes produced when the whales are at an upwards directed pitch during the day compared to the buzzes produced at night.

2.4 Discussion

The overall topic addressed by this thesis is: why do sperm whales use roll manoeuvres so actively while diving? When looking at the tag-data the whale is continuously rolling (see figures 2.2 and 2.3), either spinning around its own axis or back and forth not staying at one angle or side for long before changing its roll direction. Is there a purpose to this roll-behaviour or is it a random behaviour? Interestingly, the roll angle used by sperm whales strongly correlated with pitch angle over many of the tag deployments. Roll tended to be 'flat', falling within ±90°, when sperm whales were pitched upwards, while roll overall tended to be upside down, at angles from -180° to -90° and 90° to 180°, when sperm whales were pitched downwards as seen in figure 2.4. Because of this strong tendency, and the fact that the field of view will be affected by the pitch angle, roll behaviour was inspected separately within the different pitch modes: downward-looking, flat, and upward looking. In fact, the proportion of roll falling within LURA was found to differ statistically significantly across the different pitch modes during the search-phase for tag data recorded in all four locations.

There are great uncertainties when it comes to the amount of light present at depth where the whales are foraging during the day at the four locations. When testing if there was a change in roll-behaviour with depth, it would be more sensible to look at the changes in the actual roll-behaviour of the tagged sperm whales, rather than at what depth the light can be detected at, when trying to answer the hypothesis based on the data

used in this thesis. Comparing the roll-behaviour for day and night to test if there was a difference in the tagged sperm whales when light was available during the day and when it was not at night.

The first hypothesis, which was tested here, states that the whale is expected to be rolled at angles where it can look towards the lighter sea surface during daylight hours, if it uses vision as a principal way to look for prey or prey patches as silhouettes against the downwelling sunlight (Fristrup and Harbison, 2002). A second hypothesis concerning the use of vision while foraging when sunlight is not available, is that the whale could use vision to look for bioluminescence in their prey. In this case, the searching whale is predicted to exhibit more omnidirectional roll behaviour. If downwelling light does not provide background 'noise' in the direction of bioluminescent displays by potential prey, a higher proportion of rightside up swimming would be predicted so that bioluminescence might be seen against the darker deep-sea background (Fristrup and Harbison, 2002).

Although there are very limited data about the sensitivity of the sperm whale's eyesight, a few studies have investigated vision in the sperm whale. One study done on a stranded sperm whale eyes (Southall et al., 2002) tested for visual pigment sensitivity. Another study tested for the presence of genes coding for short-Wavelength-Sensitive cones, which make it possible to discriminate colours, in cetacean DNA, which included DNA from the sperm whale (Levenson and Dizon, 2003). The adaptation to the deep sea environment is very practical, if using vision, when spending the majority of their time at depth where the primary wavelengths present are in the blue-green wavelengths. The discrimination of colours is not that important when the only thing needed to locate bioluminescent prey by the use of vision is the actual presence of bioluminescent light, and not whether it is blue, green or flashing red. The precise levels of light found at different depths within the four study locations in this study is unknown, so calculated estimates (Douglas et al., 1998) based on Jerlov watertypes (Jerlov, 1976) are used as guidelines. Also, it should be recognized that the level of light is never constant; it changes during the course of the day, depending on the cloud cover and angle of the sun.

The sperm whales in this study were typically observed to be rolled at angles within LURA at a higher degree than expected by chance, suggesting that they have a preference to being rolled upside down or on the side when they are searching and buzzing in the bottom-interval. As argued below, the fact that the preference to be at roll-angles within LURA was not found exclusively during the day, but in the night time data as well, would indicate that the whale is not necessarily rolled upside down or on the side to use the downwelling light for vision. This interpretation is supported by lack of variation in depth in three of the four locations except for northern Norway where the whales do seem to show a slight change in depth during the search-phase, especially when they are swimming at a downward and upwards directed pitch.

2.4.1 Overall roll patterns

During the search periods in the bottom-interval of dives, looking within each location and all of the locations separately, but with no regards to depth or time of day, the whales had a general preference for swimming on the side or upside down. Within each location a Kruskal-Wallis test has shown that there is a significant difference between the pitch-modes, where whales were found to swim at roll angles within LURA at a higher proportion when they were at a downwards directed pitch in all locations except for Norway.

If the whales were capable of using the downwelling light when pitched downward, it would have to have been at a very wide angle looking towards the sea surface. This is especially true if they were not close to the surface, because of the way light is seen from depth looking towards the surface. Snell's window will be brightest right above the whale looking upwards (Land, 1990), which would not be a functional way for the whale to make use of light when in a downward pitch angle. All four locations show visibly higher proportions of roll angles within LURA when at a downwards directed pitch, indicating that the sperm whales across the locations have a tendency to be swimming downwards while being rolled almost constantly on either side and upside down as indicated by the pitch/roll graphs in figure 2.4. In Norway the whales have a significant tendency to be rolled at significantly lower proportion of roll within

LURA when being at an upwards directed pitch, which was seen as a trend the other locations as well, but not at a significant level. This result could indicate that the roll behaviour was more generally related to the search-phase rather than connected to a certain type of water at a location or be prey-related.

The same trend was seen during production of buzzes, thought to be an indicator of prey capture. The roll-pattern seen during the buzz, where the whale focusing at a specific prey or prey patch, show that they were found to be primarily on their side or upside down for all pitch-modes, indicating that no matter at what pitch the whales were at when buzzing, they preferred to be rolled at angles within the LURA, which was found for all four locations. Sperm whales at all four locations tended to have a flat pitch at the main part of the buzzes produced during the bottom-interval. When the whales were buzzing at a flat pitch, they were most typically rolled upside down or on the side, which may be an advantage during prey capture because of the way the mouth is positioned on a sperm whale. This upside down roll might make it easier for the whale to eat the prey, as suggested in Clarke and Paliza (2003) where they found a fish with toothmarks on its back in the stomach of a sperm whale which only has teeth in its lower jaw. Within the remaining two pitch-modes, a higher proportion of roll angles in LURA than would be expected of random roll movements. The whales in the Atlantic and Norway do show a higher proportion of roll falling within LURA for buzzes produced while the whales are buzzing downwards directed pitch, as seen when the whales are searching as well.

2.4.2 Day and night comparison

Overall trends in roll cannot be used to distinguish between different possible explanations for why the trend might exist. Attempting to test whether the whales showed any indication of using downwelling light for vision by comparing the way the whales rolled during the day relative to during the night. Fortunately, both day and night time data was recorded at two locations, the Gulf of Mexico and the Mediterranean, making it possible to test the data for differences. It would be expected that, if the whales at these two locations used downwelling light to visually detect prey, they would show a lower

proportion of roll within LURA at night when no light is available. For example, they might swim rightside up more at night than is observed during the day at depths where light is available.

This was clearly not the case when comparing day and night time data. In general, the distribution of roll proportions for the two locations at night does not seem to differ particularly from the daytime at these locations, and did not show any significant difference. At both locations during both day and night the whales were seen to have been at an upwards directed pitch and rolled at angles that are equal in number of dives inside and outside LURA. This means that the whales are actually spending more time rolled at angles where they are swimming rightside up during an upwards directed pitch. When the sperm whales are at a flat and downwards directed pitch while searching, they show a preference to be rolled at angles within LURA. If the whales were using the downwelling light to look for prey during the day, this would be expected, but the fact that they show the same trend at night, the possibility that the whales are rolled in that fashion during the day to make use of downwelling light as a foraging strategy seems fairly low at these locations.

This similar overall pattern was seen for the roll-behaviour during buzz production as well. The same pattern was apparent for buzzes produced in both the Gulf of Mexico and the Mediterranean irrespective of whether they were produced at day or during the night. The whales showed a strong preference to be rolled upside down or on the side, and this tendency did not show any consistent variation with changing light availability or pitch-mode. An interesting point was that across both locations, day and night, the whales spent at least some part of the all of the buzzes produced at a flat pitch rolled at angles within LURA. This shows that the absolute preference for the whales in the Gulf of Mexico and the Mediterranean were to be swimming upside down or on the side at a flat pitch when they were buzzing, during the night as well as during the day. All in all no difference was found in the roll-proportion when looking at buzzes at three different pitch-modes during the day and at night. The very clear tendency for the whales to be rolled upside down or on the side when they are buzzing at all pitch-modes and during both the day and night time, indicating that the roll-behaviour during the buzz was likely not related to the use of vision, and that the whale relies predominantly on their

echolocation for the buzz-phase, and seemed to manoeuvre to position itself in the best possible way in relation to capture prey.

2.4.3 Variations with depth for day and night dives

During the day, the whales at all four locations were rolled at angles within LURA with only minor changes with depth. The only indications of an effect of depth on rolling were seen in the Norway location which includes dives over a very large depth range. When testing the day and night comparison during the search-phase in the Gulf of Mexico and the Mediterranean, no differences in proportion of roll angles within LURA were found. This result was apparent both when testing the overall proportion of roll at each of the two locations, and when testing each of the pitch-modes separately. The way the whales are rolled during the day is very much like is seen for the majority of the time during the night as well, at a high proportion of roll angles within LURA.

At a flat pitch, the tagged whales in Norway show higher proportions of roll within LURA when they are searching at shallow depths greater than 400 meters, at which depth the proportions of roll falling within LURA seem to drop slightly to the 0.75 line. The depth difference in Norway may be consistent with the use of light during search phases when the whales are quite near the surface, which seems to disappear when the whales foraged at greater depths. Without having any night-time data in Norway, however, it is also conceivable that depth differences in roll is related to differences in prey type rather than the use of vision under conditions with insufficient levels of light. The waters off the coast of northern Norway is not categorized as the fairly clear waters found at the other three locations, meaning that here the light is attenuated faster through the watercolumn, and sunlight will not reach as far. The calculated depth, where deep sea fish can no longer detect downwelling light for a JIII watertype (Jerlov, 1976) is 200 meters (Douglas et al., 1998), which of course is only an estimate.

The roll-proportions, seen at deeper depth in Norway, which indicate roll angles falling within LURA as expected by chance. This was seen for the whales in the Atlantic as well, where the maximum depth for usable light has been calculated to be 500 meters (Douglas et al., 1998). During the day they do not show any particular change in roll-

proportion with depth, indicating that they are rolled upside down or on the side more than expected by chance as seen for the night time data as well. If they were using vision, a decrease in roll-proportion within LURA with depth would be expected, because the level of light would change within the range of depths at which they are found to forage. This should make them change their foraging strategy from the use of downwelling light rolled at high proportions of roll within LURA to more roll at angles outside LURA looking for bioluminescent prey.

When the whales are searching for prey while being at an upwards directed pitch, they are in general found to be rolling at angles outside LURA. The shallow search depths recorded from the whales in Norway continues at this pitch-mode as well, showing a high proportion of roll inside LURA, with a clear change in roll-proportion at depths deeper than 200 meters. At these deeper depths, the whales are found to be rolled predominantly rightside up when they are searching during the day. This could support the second hypothesis that the whales are rolled rightside up when looking for bioluminescence in their prey during the day against the dark seabed. As seen during the other two pitch-modes during the search-phase, the whales in the Gulf of Mexico and the Mediterranean does not show any particular change from the day time roll-behaviour, being rolled at proportions of roll angles both inside and outside LURA. These Roll-proportions could indicate a more omnidirectional roll-behaviour during the night, but because the same trend is seen during the day, the possibility of the whale choosing an omnidirectional roll-behaviour as an affect of vision is not very likely.

At the time the whale switches from the search-phase into the buzz, the whale is thought to have detected a prey and locked on to it, increasing the rate in which their echolocation clicks are being emitted (Miller et al., 2004). The whales at all four locations show the same tendency to be rolled at angles where they can look upwards towards the lighter sea surface at a higher proportion than expected by chance. A significant difference in roll proportion was found when the whales in the Mediterranean are buzzing at a flat pitch during the day compared to the buzzes produced at night. Despite this difference the buzzes produced during both day and night time are predominantly produced while the whales are rolled at angles in LURA. Therefore the

statistically significant difference could be due to the approximately three times higher sample size for day compared to night time, and the fact that daytime buzzes had a predominantly high proportion of roll angles within LURA. For the night time, the proportion of roll angles within LURA was still higher than what was expected by chance, but with less buzzes produced at proportions close to one (see figure 2.9: B) and D)). When buzzing, the whales seem to prefer staying upside down or on the side whether they are swimming upwards, flat or downwards, when there is no light available as well as during the day at any depth. This could be a clear indication that when the sperm whale has reached that final buzz, they are not using vision, but probably relying solely on their echolocation. Not even the likely change in prey types across the different field sites and foraging depths seems to have had a distinct influence on way they are rolled during production of buzzes.

The analysis in this chapter required comparing of roll behaviour of whales while searching for prey across a range of different light conditions: day versus night time and at diverse dive depths. Because no one whale provided enough data across all of these different conditions, it was necessary to pool the data from all of the different Dtag recordings from sperm whales. The risk of the results being biased because of the both the search and buzz-phases have been pooled, not taking the variance between whales into account, could be an issue when looking at the search-phase which does show some differences within locations in depth, pitch-modes and day and night separation. Though, the quite distinct difference in roll proportion of angles within LURA seen in the search-phase during the downwards directed pitch during the day compared to the night time is constant within each of the locations, which includes several individual whales, and would not be expected to be influenced much by pooling. Likewise for the very constant roll-behaviour during the buzzes, showing the similar high roll angles within LURA for all four locations, during the three pitch-modes and across the day and night separation.

Future work will include: an analysis of the search and buzz-phases collated for each individual whale as well, including the nuances for the individual whale, if present. A statistical test showing if the proportions of roll inside LURA for each of the locations at

the three pitch-modes show a difference from the proportion of roll within LURA of 0.75 as expected by chance.

On a greater scale, the chance to add some night time data to the Norway location would add great value to this thesis, possibly giving us a better indication about the way the whales in Norway are rolled when they forage when there is no light available at any depth. The nuanced results from Norway, showing indications of a change in proportion of roll angles within LURA with depth would be interesting to look into. Will they continue the shallow foraging when it is dark at the surface, or is the roll-behaviour they show solely an affect of prey?

2.5 Conclusion

The whales in this study from four different locations did not show any clear evidence of using vision as a strategy when foraging at depth. They showed a preference to be swimming upside down or on the side during both the search and buzz-phase. During the buzz the whales tended to be predominantly rolled at angles within LURA, with no regards to location, depths or whether it was during the day or night. The roll-behaviour during the day as well as night time data showed no significant difference, but similar trends within each pitch-mode, indicating that downwelling light is not a crucial factor when the sperm whale is foraging at depth during the day. Sperm whales might make use of downwelling light when it is present, but it does not appear to be a foraging strategy that determines their use of rolling body orientation.

The use of vision when the whales are foraging at depth where bioluminescence is the domination light-source is very possible, and difficult to test. The position of the whale is not as set as seen for the downwelling light, the bioluminescent organs in the prey can be placed all over the body, so all depending on if the whale is under, over or at the same depth as the prey, the position are most likely to change. Some prey species have bioluminescent organs on their ventral side to use for counter-shading, others on top of their body, meaning that there are not specific best positions for the whale, and in the dark the bioluminescence will light up in all directions.

CHAPTER 3: Does rolling in sperm whales relate to searching with echolocation?

3.1 Introduction

3.1.1 Clicking

The general perception about the regular clicks sperm whales are known to produce, when diving, is that they are used to search for prey (Gordon 1987, Jaquet et al., 2001, Wahlberg 2002, Madsen et al. 2002b, Miller et al. 2004). In a study done in the western Mediterranean Sea, Drouot et al. (2004) found that the sperm whales started producing regular clicks as soon as 8 sec after leaving the surface while others started after 3 min, with an average of 1 min and 11 sec during the descent phase. Animals from the same study continued clicking all the way up to between 4 min 48 sec and 8 min 36 sec before surfacing (Drouot et al., 2004). In Watwood et al. (2006) they found the sperm whales in the Gulf of Mexico, the Atlantic and the Mediterranean to start clicking at 97-225 meters after leaving the surface, and to stop again at a mean time of 2 minutes into the ascent, where Zimmer et al. (2003) tagged a sperm whale in the Ligurian Sea in the western Mediterranean, and found this whale to start clicking at a depth of 100 meter and not to produce any clicks during the entire ascent phase. Whales recorded in other areas like off the coast of Kaikoura, New Zealand were found to begin the regular clicks within 25 seconds after leaving the surface, and when returning to the surface, they did not produce clicks for the remaining three to four minutes before reaching the surface (Jaquet et al., 2001). In Norway, Madsen et al. (2002b) reports that the male sperm whales found here, start to produce regular clicks after 30-60 seconds at a depth of 50-250 meters and continues until it reaches the last few 100 meters before reaching the surface.

Some researchers have presented theories about why the sperm whales begin the regular clicks early in the descent, and what information the regular clicks can give the whale so early on in the dive. Zimmer and colleagues (Zimmer et al., 2003) found that the Inter Click Intervals (ICI) from a tagged sperm whale in the Mediterranean, decreased

with depth and seen to show slight changes correlated with fluctuations in animal pitch when whales were at an overall downwards directed pitch during the descent. This, they hypothesize, could be because the whale has begun searching for or detecting horizontally dispersed prey within a target depth layer at an early point in the descent. A similar type of change in ICI was found in a study off Papua New Guinea in tagged sperm whales, which showed the same tendency of decreasing ICI with depth, indicating that the whale is continuously detecting something or searching at a specific depth (Madsen et al., 2002a) or all the way to the seabed as found in Thode et al. (2002). This strategy would make sense because as they found in (Madsen et al., 2002) it should be possible for the sperm whale to detect some prey species at up to 500 meter using regular clicks. The theory of echolocating whales predetermining the depth layer they want to search at is suggested by Aguilar Soto et al. (2006), for short-finned pilot whales off Tenerife, as well.

The use of regular clicks varies with the different locations as found in the examples above. In Norway the whales have been found to start producing regular clicks at shallow depths and to continue clicking during the ascent (Madsen et al., 2002b, Teloni et al., 2008) which is probably explained by the fact that the mature males found at these latitudes, forage at depths as shallow as 17 meters where buzzes have been recorded (Teloni et al., 2008). This would make it sensible for the whale to start searching at a shallow depth as well, looking for prey soon after they leave the surface, and during ascent from greater depths.

3.1.2 Manoeuvring

As described in Chapter 2, sperm whales are very active when diving, with frequent changes in the body orientation. This is especially clear from tag-data where they are seen to continuously change their body roll for the majority of the time when they are diving.

The use of roll seems to be a strategy for several marine mammals, possibly related to prey capture or to searching behaviour. A fairly clear example of roll orientation during prey capture is reported for lunge-feeding baleen whales. Finwhales

(*Balaenoptera physalus*) in Southern California Bright modify their body roll orientation as a part of their lunging behaviour (Goldbogen et al., 2006). They found that some finwhales use the roll during a lunge as a foraging strategy, some only forage using the roll lunge, also referred to as a lateral lunge. Others mix between the regular lunge without the roll, and lateral lunges that includes rolls over 45º, while the remainder only use the lateral type of lunge. Both lunge types have been reported by Gaskin (1982) in Nova Scotia as well, who suggested that the lateral lunge is more effective, and probably the better strategy for catching euphuasiids rather than fish.

Variations in rolling orientation have also been observed during searching behaviour. Narwhals (*Monodon monoceros*) were tagged with DTAGs and a crittercam in the Admiralty Inlet in Canada (Dietz et al., 2007). In this study they found that of the two animals tagged with a Dtag, one was found to be spinning all the way to the maximum depth of the dive while the second one to be swimming upside down during most of the descent. During the ascent, one Narwhal was rolling slightly and then continued right side up the remainder of the ascent, while the other one was spending almost the entire way to the surface rolled rightside up. For the rest of the dives they were found to be rolling upside down for over half of the time diving, especially when at the bottom, they were turned upside down for the majority of the time. No evidence of feeding was found, however, on neither the crittercam or from the acoustic files from the Dtag (Dietz et al., 2007).

In a species of toothed whales, the finless porpoise (Neo*hocaena phocenoides*), Akamatsu et al. (2009) found that the porpoises show two types of dives; the 'roll'-dive, that shows a pronounced roll-behaviour, and an extensive use of sonar, which is closely connected to foraging. Limited use of sonar was observed during the second type of dive, the normal 'upright' dives, where the porpoise stayed at angles between ± 60 degrees for the majority of the time (Akamatsu et al., 2009). Sperm whales are reported to increase their rolling behaviour during the production of buzzes, which is thought to indicate a prey-capture attempt (Miller et al., 2004), but variations in rolling behaviour in other phases of the sperm whale dive have not been investigated.

3.1.3 Echolocation beam

A possible reason why toothed cetaceans might increase rolling activity during echolocation search behaviour is to increase the search area (Akamatsu et al., 2009). Increased variation in roll angles could result if changes in roll are needed for the clicking animal to change its direction of movement. Alternatively, even without changes in the direction of movement, if the sonar beam is emitted at an angle somewhat off the body axis, changes in roll could result in a wider overall search area, which would be affected by roll when the whale is emitting clicks. For some species like the bottlenose dolphins (Tursiops truncatus) and harbour porpoises (Phocoena phocoena), the echolocation beam is directed slightly off the body axis (Au et al., 1999), and not emitted from the melon in a straight forward direction. The same tendency was found in the Beluga whale (*Delphinapterus leucas*) with a beam axis directed 5 degree upwards (Au et al., 1987), and Philips et al. (2003) found that the echolocation beam of the Risso's dolphin (*Grampus griseus*), as seen in bottlenose dolphins, harbour porpoise and the beluga whale, was off axis, but at a downward directed angle.

A study by Zimmer et al. (2005) produced an estimated transmit beam pattern describing the distribution of nearly 13000 regular clicks from a sperm whale tagged with a Dtag in the Ligurian sea in the Mediterranean. This beam pattern shows a spreading around the 0º azimuth and 0º elevation with high peak levels out to +20º and almost -40º in elevation, and +20º to -25º azimuth (Zimmer et al., 2005). Because of the very limited amount of data showing how the sonar beam of the sperm whale is emitted, and because of the difficulties of doing such studies on wild animals, it cannot be ruled out that the sperm whale beam pattern may in fact be somewhat off axis. Measurements of roll taken from the sensor-data as well as the acoustics recorded on the Dtag might help give some indications of how sperm whales change orientation with respect to clicking behaviour at depth, when the sperm whale is searching for prey.

The aim of this chapter was to test whether the tagged sperm whales in this dataset show an increase in changes in roll after they start clicking versus before start of clicking during the descent, or after during clicking versus after clicking stops during the

ascent. The data used are from all four different locations in which Dtag data have been collected: the Gulf of Mexico, the Atlantic, the Mediterranean and northern Norway. Increases in changes in roll would be clearly reflected in the variation of observed roll angles, so the observed variation in roll during clicking periods is compared with the silent time-interval when the whale leaves the surface until it starts clicking during the descent. During the ascent the variance in roll when the whale is producing regular clicks is compared to the time-interval when it stops clicking on its way to the surface and till it actually surfaces. The hypothesis tested is that the whales exhibit a higher variance of roll, meaning that they are changing their rolling more, when they are clicking. The null hypothesis is that rolling behaviour is independent whether or not the whale is clicking. If rolling behaviour is linked to whether or not a whale is clicking, this would suggest that rolling is beneficial during echolocation-based searching for prey at depth.

3.2 Materials and Methods

3.2.1 Data

Descent and ascent periods for dives from 46 and 48 sperm whales, respectively, were used for the analysis in this chapter. The acoustic recordings as well as the orientation sensor-data from the Dtag were used, as described in the previous chapter. The sperm whales were tagged in four different locations: the Northern part of the Gulf of Mexico in July 2001, August-September 2002 and June 2003 (25 tags); the Ligurian Sea in September –October 2001, July 2002 and September 2003 (9 tags); the North Atlantic in July 2003 (7 tags); and in Northern Norway in July 2005 and May and June in 2008 and 2009 (6 tags). All data processing and analyses have been performed in Matlab version 6.5 and 7 (Math Works).

The foraging dives performed by the tagged whales from all four locations were separated into three phases (as in Chapter 2); the descent phase starting when the whale leaves the surface and continues until the whale changes its pitch to 0 degrees where the bottom phase begins. The bottom phase ends when the whale showed an upwards directed pitch after the last downwards directed pitch. This is the beginning of the ascent

as well, which ends when the whale reaches the surface (defined in Miller et al., 2004a). Specific criteria were used for each dive to determine whether or not to include it in the analysis.

Descent-phase:

1) To enable good quantification of variation in roll, the time-interval from when the whale leaves the surface to the time when it starts producing regular clicks is longer than 60 seconds.

2) Similarly, the time-interval from when the whale starts producing regular clicks to the time the whale levels out at depth and the bottom-phase begins, is longer than 60 seconds.

Ascent -phase:

1) Again to enable good quantification of variation in roll, the time-interval from when the foraging-phase ends and the whale swim toward the surface to the time when it stops producing regular clicks has to be longer than 60 seconds.

2) Similarly, the time-interval from when the whale stops producing regular clicks to the time the whale reaches the surface is longer than 60 seconds.

In case of a descent not meeting the criteria, either because the whale produced regular clicks soon after leaving the surface, thus not fulfilling the minimum of a 60 sec time interval of not-clicking roll-behaviour, or that the whale starts clicking very late in the descent phase, the problem becomes that there is too little roll-data where the whale is clicking before starting the bottom phase. The reason why the data from the bottom phase is not included in the analysis is that the roll-behaviour during bottom-phase foraging might be influenced by other factors than occur during descent or ascent. As described in the previous chapter, one such function could be that the whales could be using roll as a foraging strategy using vision as an aid to echolocation during foraging. Alternatively changes in roll could reflect requirements for prey capture (Miller et al., 2004).

After analysing the individual dives, many were found to have only a descent or an ascent meeting the criteria, but in a few dives both the descent and the ascent were

accepted for analysis. Two examples are shown in figure 3.1 and 3.2, where one dive is shown, with a blue x and a vertical broken line marking the start of the regular clicks found on the acoustic recordings from the Dtag. The red x and vertical broken line shows the end of the regular clicks during the ascent phase, and marked in green is the roll angles from the sensor-recordings. In figure 3.1 the descent would be discarded because the whale start to produce regular clicks very less than a minute after leaving the surface, which has been set as a criteria to ensure that there are a sufficient number of samples to test the hypothesis. This scenario is seen fairly often, and not just in the descent phase, but during the ascent as well, where the whale continues to produce regular clicks all the way to the surface.

Out of the 371 full dives in the tag-records, 202 descent and 206 ascents met the criteria set to test the hypothesis.

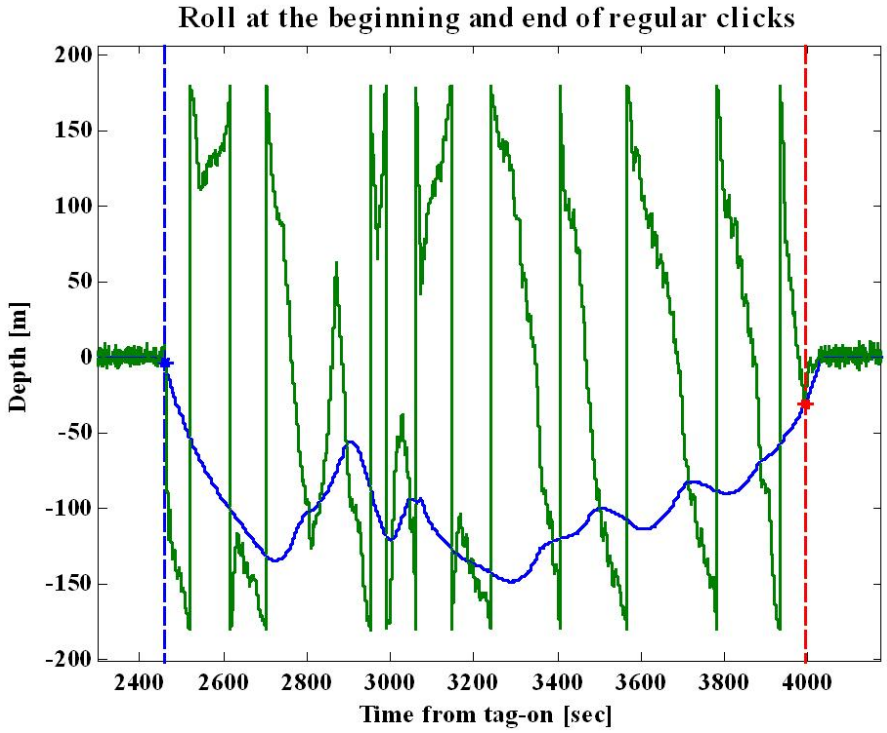

Figure 3.1 Dive profile from a shallow foraging dive from Norway (sw09_142a) with the seconds after the tag was attached to the whale on the x-axis, and the dive depth at the lower part of the y-axis with the upper part showing the roll angles (shown in green) ranging from -180 to 180, negative values are left-side roll and positive illustrates the roll-angles to the right side. The blue x and the broken line mark the beginning of regular clicks, and the red shows the end of the clicking along with the red broken line.

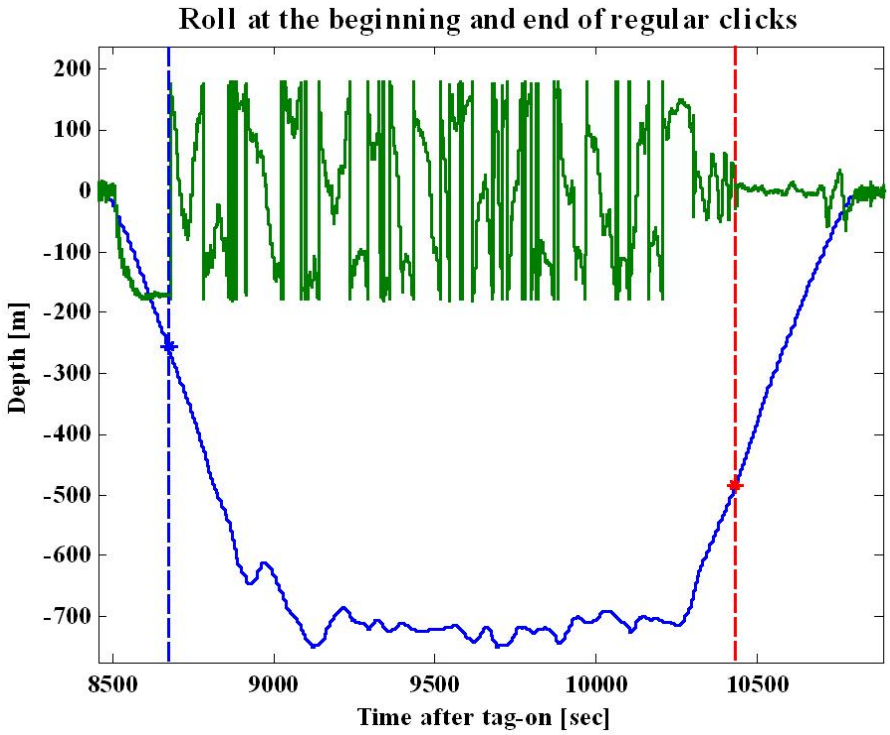

Figure 3.2 Dive profile from a deep foraging dive from the Gulf of Mexico (sw01_204) with the seconds after the tag was attached to the whale on the x-axis, and the dive depth at the lower part of the y-axis with the upper part showing the roll angles (shown in green) ranging from -180 to 180, negative values are left-side roll and positive illustrates the roll-angles to the right side. The blue x and the broken line mark the beginning of regular clicks, and the red shows the end of the clicking along with the red broken line.

In this second example of a dive (figure 3.2), both the descent and the ascent can be used for analysis.

Comparison of the amount of variation in roll was done using the same number of samples on either side of the start of the regular clicks during the descent phase and the end of the clicking during the ascent, which can vary somewhat for each individual dive. After the selection of which descents and ascents can be included in the analysis, the measured roll-angles for each dive for one whale during the descent phase were pooled and then analysed. In the analysis, the variance of the measured roll is used as the dependent factor. The variance (s) is calculated from Rayleigh's r-vector (r), which is also referred to as the mean-vector (Zar, 2010), which is a measure of concentration for the mean angle in circular statistics and ranges from zero to one. A low r-vector shows that the data are very dispersed with a great variance. The opposite scenario is a mean-vector near 1.0, indicating a high directionality of angles and hereby a low variance.

3.2.3 Statistics

A non-parametric paired Wilcoxon test was used to test if there were any significant differences in the variation in roll before production of regular clicks, compared to the same time-duration after the regular clicks have started during the descent. An identical test was used to test the roll-behaviour during the ascent before the whale ends the regular click and compare it to the time with no clicking before the whale reaches the surface again.

The variation in roll was calculated for each of the descent and ascent phases for the individual dive, with no regard to the individual whale, and then later separated into each of the four locations to look if there were any geographical differences in the roll-variance during clicking. The same test was done for each of the individual whales, again first the overall tendency, ignoring location, and afterwards separated into locations and tested one location at a time. Because the value tested statistically in this chapter is the variance of all the roll samples from a descent or an ascent, the importance of independence samples is not as great as if the individual samples were pooled. All the tests have been tested at a significance-level of $\alpha=0.05$. The non-parametric paired Wilcoxon statistical tests were done in CYSTAT version 10 (SPSS Inc.)

3.3 Results

The dives used for the analysis in this chapter have been sorted from a larger number of dives from all four of the locations. As described in the previous section, the dives were cut because they did not meet a certain set of standards to make it possible to test the hypothesis. The analysis was performed on two separate ways of looking at the data-set: 1) analyse the mean-value for the descent and the ascent phases for each whale taking the variability within the data-set into account, 2) analyse the data-set by separate dives, not considering the variability within each whale.

Table 3.1 The number of whales and dives used for the analysis of roll behaviour when the tagged whale was producing regular clicks and when it was not producing regular clicks during the Descent and Ascent phase.

	Individual dives		Individual whales	
	Descent phase	**Ascent phase**	**Descent phase**	**Ascent phase**
Gulf of Mexico	124	94	24	25
The Atlantic	16	12	7	6
The Mediterranean	31	50	9	10
Norway	31	50	6	7
All locations	202	206	46	48

3.3.1 Analysis of individual dives

When the whale starts the descent phase of a dive, they start to produce regular clicks. Some start shortly after fluke out, others wait until they reach a greater distance from the surface before starting the regular spaced clicks well known for sperm whales. The x-axis shows the number of dives analyzed. The variance (s) ranges from 0-1 where 0 represents a low variance, that the whale were rolled at angles in the same direction, whereas a high variance means a less directional distribution of roll angles, and that the whale have a more diverse roll-pattern.

3.3.1.1 All locations combined

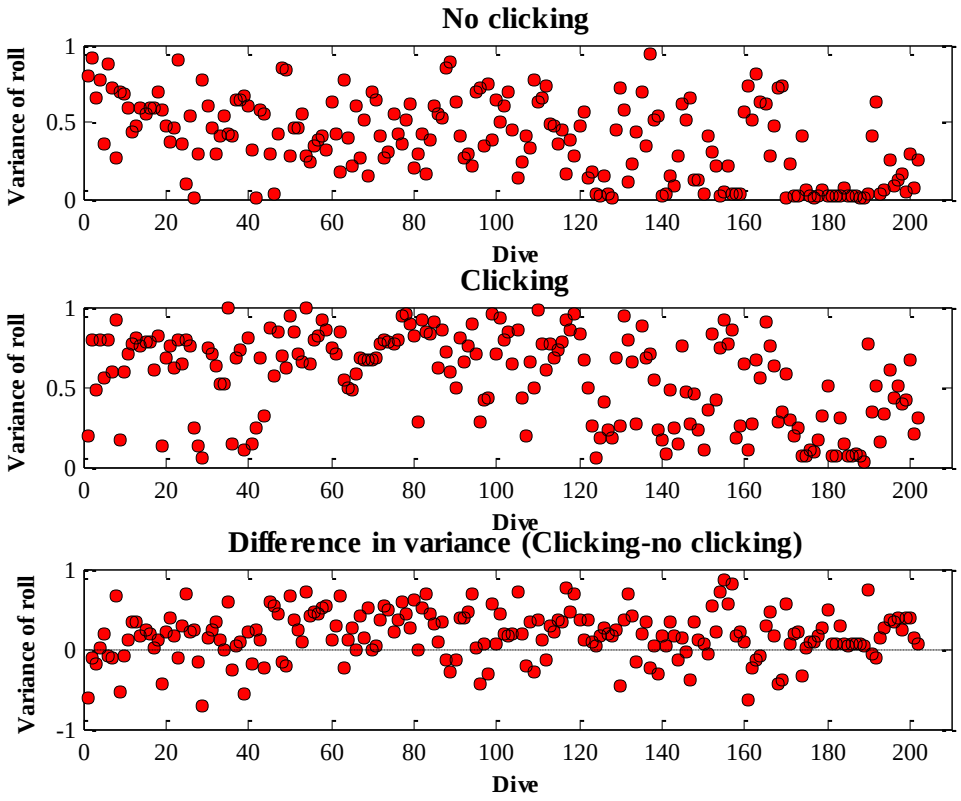

Figure 3.3 Variance of roll for the Descent phase. In the top-plot the variance of roll is shown for the descent phase before the whale begins the regular clicks, with the individual dives in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll after the whale has started the regular clicks during the descent phase, and the bottom plot shows the variance during clicking minus the variance during no clicking plotted as either a positive or a negative difference in variance.

Looking at the top-plot in figure 3.3 the distribution of roll variance is centered on the 0.5 line with outliers both at zero as well as close to one, which indicates that the whale does show some variance in roll before they start clicking after leaving the surface. The variance of roll when the whale has started producing the regular clicks shows a higher variance above the 0.5 line for the majority of the descent-phases, and looking at the difference in variance in the bottom plot, does show a difference in the majority of the descent phases between the roll when the whale is clicking compared to when it has not begun producing clicks. This tendency has been supported by the statistics that show that there is a significant difference in roll-variance between the “no clicking” and “clicking”, where descents show more varied roll-behavior during clicking in 155 of a total of 202

descent-phases (Wilcoxon non-parametric paired test: Z=7.314 p=0; n=202; mean $s_{noclicking}$ = 0.3859; mean $s_{clicking}$ = 0.5604).

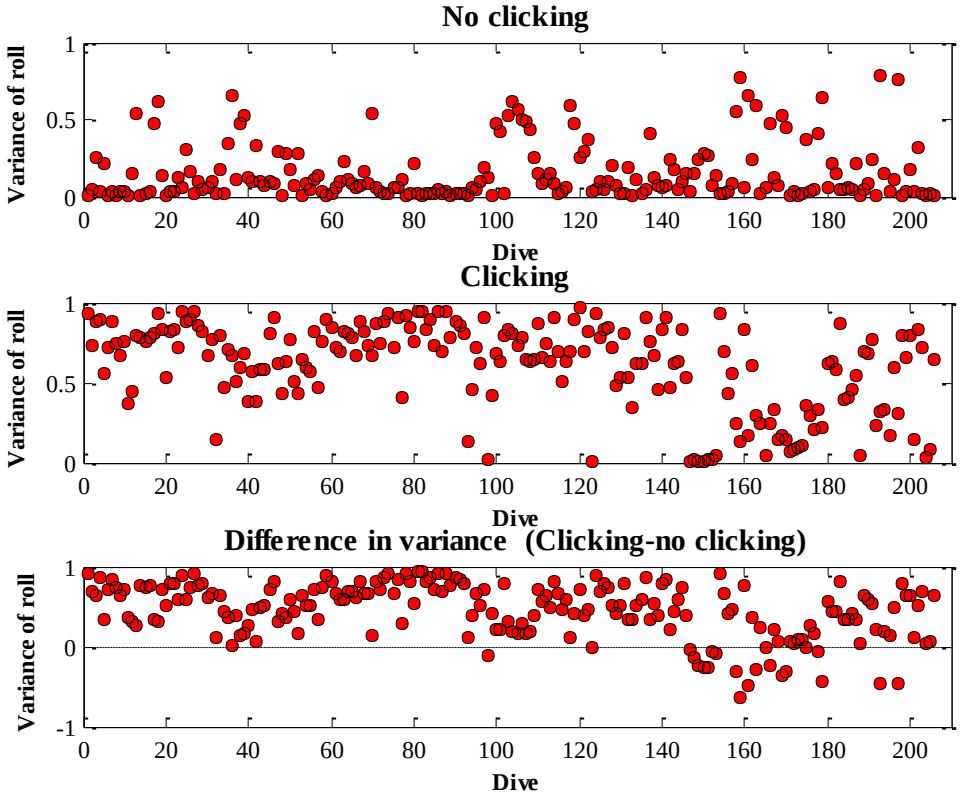

Figure 3.4 The variance of roll for the Ascent phase. In the top-plot the variance of roll is shown for the ascent phase after the whale stops producing regular clicks, with the individual dives in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll before the whale has stopped the regular clicks on its way to the surface. The bottom plot shows the variance during clicking minus the variance during no clicking plotted as either a positive or a negative difference in variance.

The plots illustrating the roll variance during regular click production compared to when the whales were not clicking during the ascent-phase, shows a very clear picture for the majority of the ascents. During clicking when the whale was on its way towards the surface the variance in roll is predominantly high. During the time periods before the whales reached the surface, but were no longer producing regular clicks, the data shows a very low roll-variance, indicating that the whales stay predominantly at the same roll angles when they were not clicking. In the bottom plot, the difference between the "clicking" and "no clicking" periods is clearly high for the majority of the ascent-phases, but does show a few ascent-phases where the difference is less pronounced. The overall tendency of a distinct difference in roll-variance during the ascent-phase when the whale

is clicking compared to when it not, is once again seen in the statistics as well (Wilcoxon non-parametric paired test: Z=-11.301 p=0; n=206; mean $s_{noclicking}$ = 0.1545; mean $s_{clicking}$ = 0.6057) that show that the difference in roll-variance is significantly different from each other.

3.3.1.2 Inter-location analysis

Because the overall analysis of the roll-variance for both the descent and ascent-phase showed a highly significant difference between the roll-behaviour when the whales are clicking compared to when they are not, it would be interesting to see if the same tendency is found within each of the four locations.

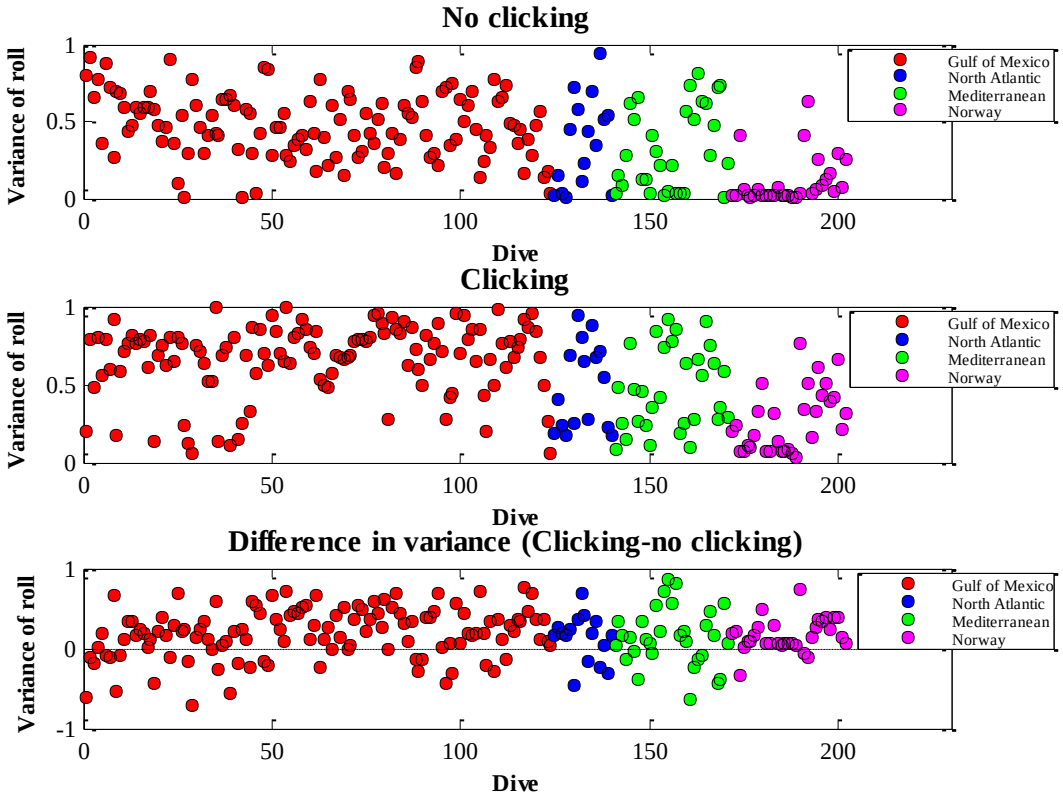

Figure 3.5 The variance of roll for the Descent phase for each of the four locations. In the top-plot the variance of roll is shown for the descent phase before the whale begins the regular clicks. Each location is marked by different colours; Gulf of Mexico is shown in red, the Atlantic in blue, the Mediterranean in green and Norway in magenta. The individual dives are seen in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll for each location after the whale has started the regular clicks during the descent phase, and the bottom plot the difference between the two given variances of roll plotted as either a positive or a negative change in variance shown in different colours to separate the locations.

The top plot shows the roll-variance for individual dives during the descent-phase, from tagged whales from all four locations. Comparing the roll-variance for the Gulf of Mexico before the whale begins the regular clicks, the tendency shows that the roll-variance is centered on the 0.5 line for the descent-phase with a distinctively higher variance once the clicking has started. Statistically the test shows that there is a significant difference in roll-variance when the whale is not producing regular clicks to when it is (Wilcoxon non-parametric paired test: Z=5.967 p=0; n=124; mean $s_{noclicking}$ = 0.4733; mean $s_{clicking}$ = 0.6651) where 94 of the 124 descents had a higher variance when the whales were clicking than when they were not.

A different pattern is shown for the Atlantic, where the roll-variance for both the "clicking" and the "no clicking" show a wider distribution, some descents with a low variance in roll-behaviour and some with high variability. Looking at the difference in the bottom plot, it does show a number of differences close to zero and others further away on either side of the zero, indicating that more descents had a higher variance of roll when they were clicking, the positive differences, than when they were not producing regular clicks during the descent. Testing the results with a non-parametric paired Wilcoxon test, it shows that there is no significant difference between the two even though there are more descents with a higher variance when the whales are clicking compared to the time when they are not (Z=1.551 p=0.121; n=16; mean $s_{noclicking}$ = 0.3626; mean $s_{clicking}$ = 0.4871).

In the Mediterranean the whales show a very widely distributed pattern as well, but with a slight tendency for a lower variance when they were not clicking compared to the variance seen in the middle plot, where the whales were producing regular clicks. The difference between the "clicking" and "no clicking" was statistically significant (Wilcoxon non-parametric paired test: Z=2.058 p=0.040; n=31; mean $s_{noclicking}$ = 0.3288; mean $s_{clicking}$ = 0.4707) with 21 out of the total 31 descents showing a higher variance of roll, as seen in the bottom plot as well.

For the final location, Norway, the variance of roll shows a very different pattern than seen for any of the other three locations. When the whales were not clicking, the variance of roll was very low for the majority of the descents, with a number of descents showing a more varied distribution of variance. This means that there is very little change

in the roll behaviour during the descent in Norway, when the whales were not clicking. When the whales began producing regular clicks as it dives deeper, the tendency for the variance to be very low continues, but with a larger number of the descents showing an increase in roll-variance, resulting in a significant difference between the "no clicking" and "clicking" (Wilcoxon non-parametric paired test: Z=3.919 p=0; n=31; mean $s_{noclicking}$ = 0.1052; mean $s_{clicking}$ = 0.2687) with 28 of the 31 descents showing a higher variance when the whales were producing regular clicks.

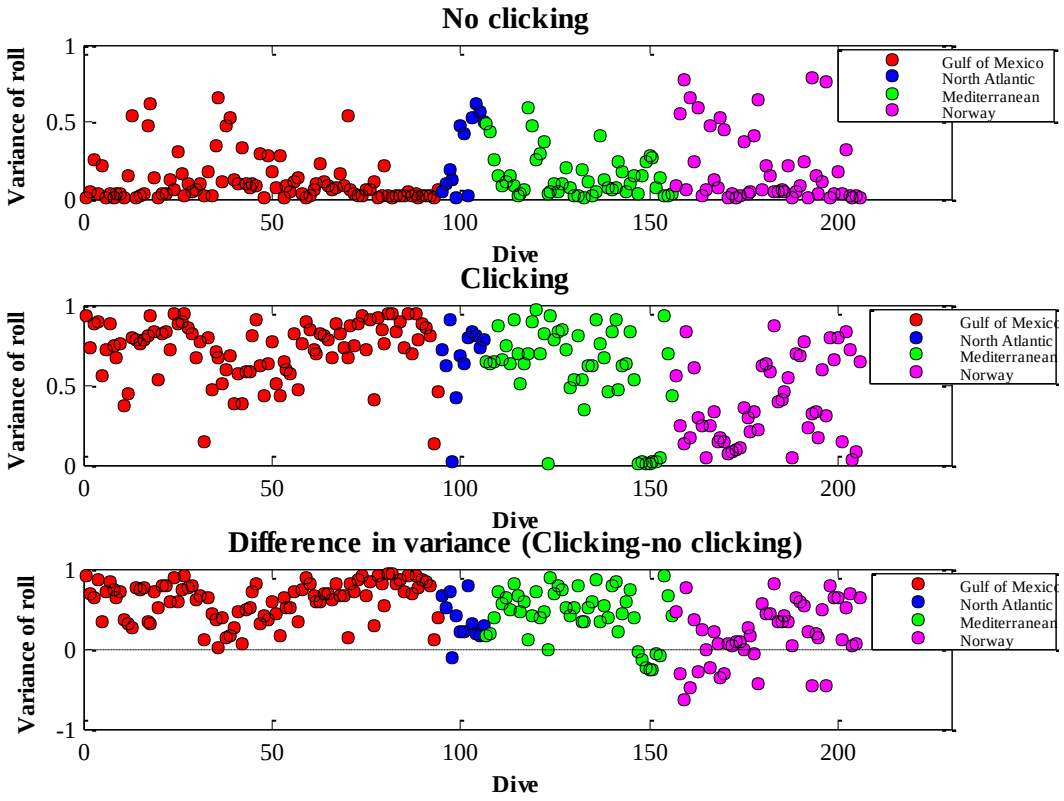

Figure 3.6 The variance of roll for the Ascent phase for each of the four locations. In the top-plot the variance of roll is shown for the ascent phase after the whale stops producing the regular clicks. Each location is marked by different colours; Gulf of Mexico is shown in red, the Atlantic in blue, the Mediterranean in green and Norway in magenta. The individual dives are seen in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll for each location before the whale has stopped producing the regular clicks during the ascent phase, and the bottom plot the difference between the two given variances of roll plotted as either a positive or a negative change in variance shown in different colours to separate the locations.

When the whale starts the ascent and swims toward the surface, it continues to produce regular click for a time which varies greatly from some whales clicking almost all the way to the surface, where others stop clicking shortly after starting the ascent.

The clear pattern seen for the ascents from the Gulf of Mexico is seen in the middle plot, with predominantly high roll-variances, and very low variances when it was not clicking in the top plot. When comparing these, a very clear pattern emerges where all the ascents at this location show a higher variance of roll when the whale is clicking on its way to the surface (Wilcoxon non-parametric paired test: Z=-8.419 p=0; n=94; mean $s_{noclicking}$ = 0.1149; mean $s_{clicking}$ = 0.7244).

In the Atlantic, the tendency for the ascent when the whales were clicking is that they seem to roll over a larger distribution of angles when they are producing regular clicks, seen as a high variance of roll in the middle plot. When they stopped clicking on the other hand, the variance decreases to a variance of 0.5 or less, so by comparing and looking at the difference, it shows that the whale does seem to have a greater variance of roll when the whales are producing clicks, which is supported by the statistics showing that the difference in roll-variance is significantly different (Wilcoxon non-parametric paired test: Z=-2.981 p=0.003; n=12; mean $s_{noclicking}$ = 0.2998; mean $s_{clicking}$ = 0.6618).

Looking at the ascents in the middle plot for the Mediterranean, the majority of the ascents does show a variance at 0.5 or above, except for a few outliers at very low roll-variance close to zero. When the whales stopped clicking on their way to the surface, the variance during the ascent is found to be predominantly low. As seen for the previous two locations, the difference between the “clicking” and the “no clicking” is primarily the variance in roll being higher during the regular clicks, with the difference being statistically significant (Wilcoxon non-parametric paired test: Z=-5.681 p=0; n=50; mean $s_{noclicking}$ = 0.1507; mean $s_{clicking}$ = 0.5901).

When regular clicks were produced during the ascent in Norway, the variance of roll shows a different pattern than seen at the other three locations. Here, the variance of roll is less consistent, with some whales rolling more, showing high variance, some have a directional roll-behaviour with low variance and other have a variance in between. During the ascent when the whale is not clicking, the whales tended to roll less, shown as a low roll-variance, making the difference in variance larger with 37 of the 50 ascents

having a higher variance of roll when the whale is clicking (Wilcoxon non-parametric paired test: Z=-3.248 p=0.001; n=50; mean $s_{noclicking}$ = 0.1980; mean $s_{clicking}$ = 0.3845).

3.3.2 Individual whale analysis

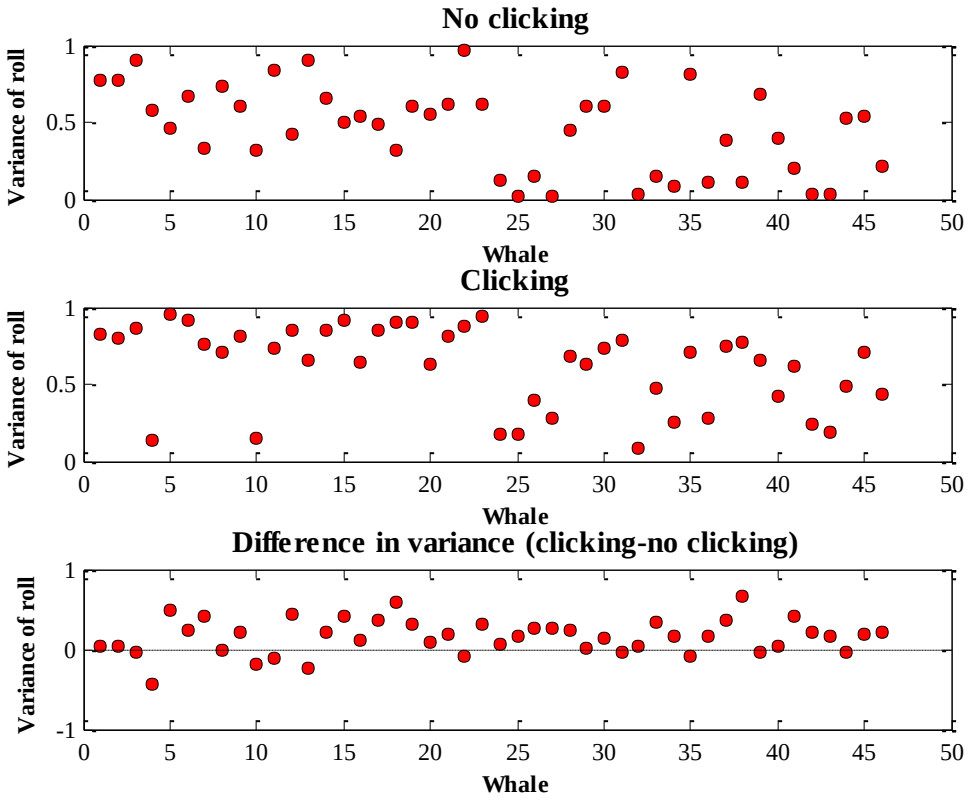

Figure 3.7 The variance of roll orientation for the Descent phase. In the top-plot the variance of roll is shown for the descent phase before the whale begins the regular clicks, with the individual whale in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll after the whale has started the regular clicks during the descent phase, and the bottom plot the difference between the two given variances of roll plotted as either a positive or a negative change in variance.

When looking at the variance of roll within each of the whales, the overall tendency seems very much like what was seen when looking at the individual dives. In the top plot, the first half of the whales show a roll-variance close to 0.5 or higher, where the last half have more whales at a low variance below 0.5, meaning that they showed more directionality before starting the regular clicks on their way to forage. On the other hand when the whales start the regular clicking, the first half of the whales show a predominantly high variance of roll, whereas the second half have a wider distribution of

variance centered at 0.5. To see if there is a difference between "no clicking" and "clicking" the bottom plot shows that the whales do have a majority of higher variance of roll when they are clicking during the descent phase compared to the time before they start the regular clicks when first leaving the surface (Wilcoxon non-parametric paired test: Z=4.081 p=0; n=46; mean $s_{noclicking}$ = 0.4619; mean $s_{clicking}$ = 0.6178).

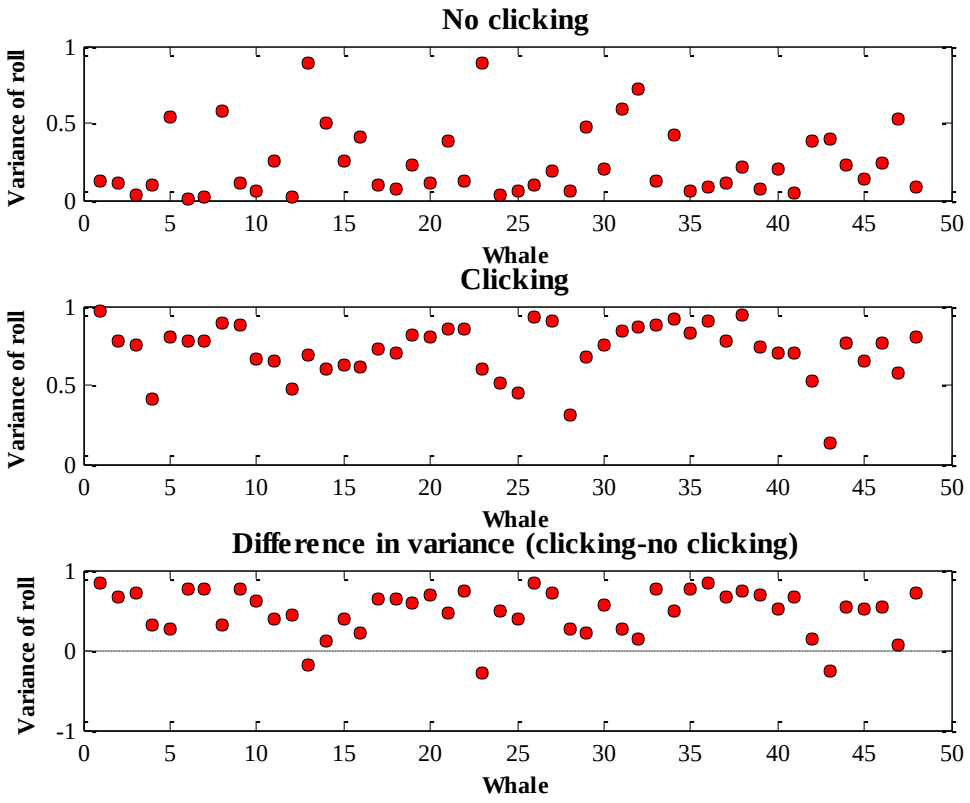

Figure 3.8 The variance for the Ascent phase. In the top-plot the variance of roll is shown for the ascent phase after the whale stops producing regular clicks, with the individual whale in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll before the whale has stopped the regular clicks on its way to the surface. The bottom plot shows the difference between the two given variances of roll and is plotted as either a positive or a negative change in variance.

During ascent, the variances of roll for the tagged whales seem to show the same overall tendency. As seen in the middle plot, the variance is predominantly higher than 0.5, meaning that the whales tend to roll more when they were clicking during the ascent-phase. Another very clear trend shows in the top plot with a generally very low variance for the majority of the tagged whales, which indicates that the whales show a very limited roll-behaviour when they were not producing regular clicks on their way towards the

surface. When testing the difference in roll-variance between "clicking" and "no clicking", the statistics show as well as seen in the bottom plot, that the difference in roll-variance is significantly different, with 45 out of 48 ascents having a higher variance of roll (Wilcoxon non-parametric paired test: Z=-5.744 p=0; n=48; mean $s_{noclicking}$ = 0.2422; mean $s_{clicking}$ = 0.7220).

3.3.2 Individual whale by location analysis

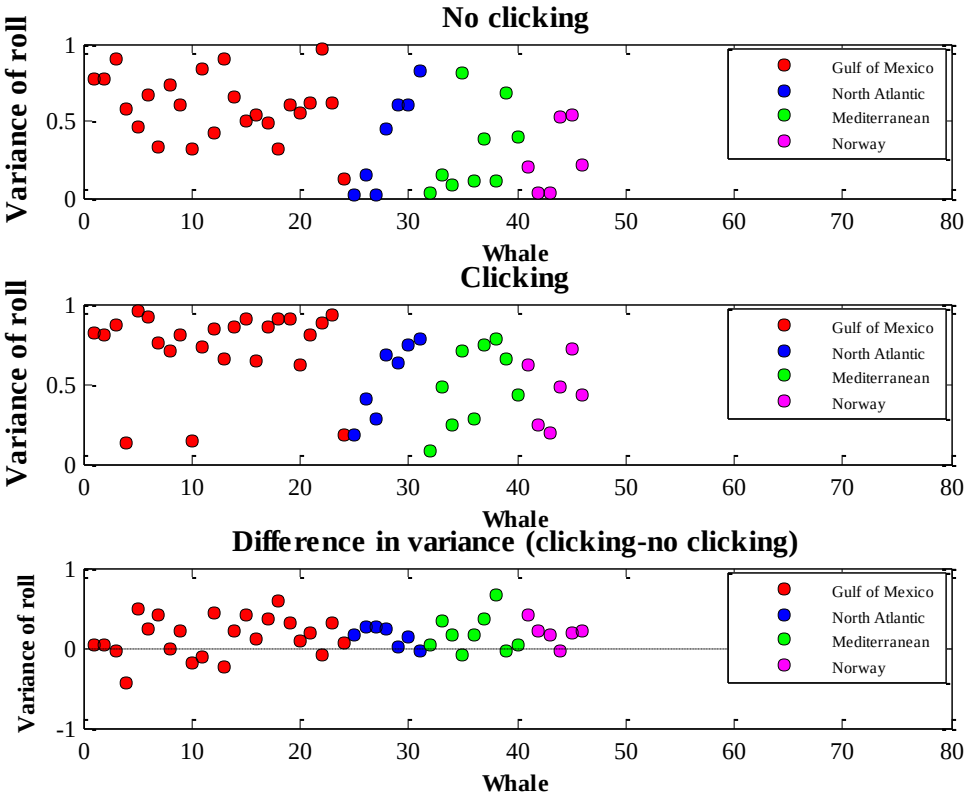

Figure 3.9 The variance in roll for the Descent phase for each of the four locations. In the top-plot the variance of roll is shown for the descent phase before the whale begins the regular clicks. Each location is marked by different colours; Gulf of Mexico is shown in red, the Atlantic in blue, the Mediterranean in green and Norway in magenta. The individual whales are seen in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll for each location after the whale has started the regular clicks during the descent phase, and the bottom plot the difference between the two given variances of roll plotted as either a positive or a negative change in variance shown in different colours to separate the locations.

The combined data from the descents within each of the tags show a similar trend as the one seen for the descent during the individual dives. The whales tagged in the Gulf of

Mexico were found to have a widely distributed pattern of roll-variance centered on 0.5 when they were not clicking when starting the descent. When they do start producing regular clicks, the variance of roll increases and are seen as predominantly high variances of roll in the middle plot, except for three outliers having fairly low variances during clicking while descending. The difference in the way the whales are rolled when they are not clicking compared to when the are not, does show a higher variance in 17 of the 24 descents, and statistically there is a significant difference in the variance when the whales are clicking and when they are not (Wilcoxon non-parametric paired test: Z=2.429 p=0.015; n=24; mean $s_{noclicking}$ = 0.5947; mean $s_{clicking}$ = 0.7355). In the Atlantic, the variance of roll when the whales are not clicking seem to be at 0.5 and higher with a few outliers at very low variances of roll, whereas when the whales start the regular clicks, the whales are found to be scattered at both high and low variances of roll. Of the 7 descent from this location, 6 have shown to have a higher variance of roll, and statistically there is a significant difference between "no clicking" and "clicking" (Wilcoxon non-parametric paired test: Z=2.028 p=0.043; n=7; mean $s_{noclicking}$ = 0.3822; mean $s_{clicking}$ = 0.5270). The whales from the Mediterranean have variances of roll predominantly below 0.5 when they are not clicking during the descent-phase, and when they start to click the variance increases and more whales are found to have a variance at 0.5 and higher, with a few whales having a less varied roll-behaviour when they click during the descent. Looking at the difference between the roll-variance when the whales are clicking compared to when they are not producing regular clicks, 7 of the 9 descents have a higher variance when the whales are clicking (Wilcoxon non-parametric paired test: Z=1.955 p=0.051; n=9; mean $s_{noclicking}$ = 0.3067; mean $s_{clicking}$ = 0.4894) but the difference between "no clicking" and "clicking" were not significant. The pattern seen for the whales in Norway is very similar to what was seen in the Atlantic. Here, the whales show variances that are low as well as having some outliers at a higher variance when the whales are not producing regular clicks during the descent. When the whales are clicking, they show a varied variance of roll shifted to a lower variance centered at 0.5, resulting in the difference in variance of roll between the "clicking" and "no clicking" to be predominantly the same for all the tagged whales. This difference was found to be significantly different, showing a higher variance of roll when the whale is

clicking during the descent (Wilcoxon non-parametric paired test: Z=1.992 p=0.046; n=6; mean $s_{noclicking}$ = 0.2563; mean $s_{clicking}$ = 0.6178).

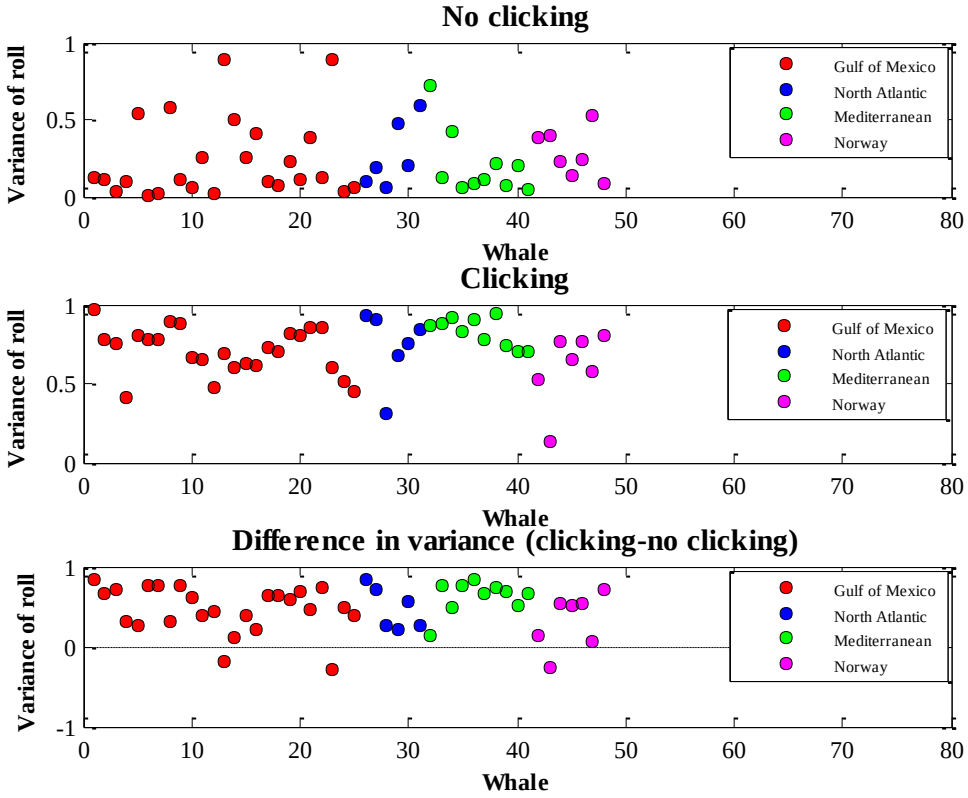

Figure 3.10 The variance in roll for the Ascent phase for each of the four locations. In the top-plot the variance of roll is shown for the ascent phase after the whale stops producing the regular clicks. Each location is marked by different colours; Gulf of Mexico is shown in red, the Atlantic in blue, the Mediterranean in green and Norway in magenta. The individual whales are seen in the x-axis and the variance of roll from zero to one on the y-axis. The middle-plot illustrates the variance in roll for each location before the whale stops the regular clicks during the ascent phase, and the bottom plot the difference between the two given variances of roll plotted as either a positive or a negative change in variance shown in different colours to separate the locations.

The tendency seen for the whales clicking on their way to the surface in the Gulf of Mexico is that they show a high variance of roll for the majority of the whales, with all whales except for two, having a variance higher than 0.5. When the whales stop producing clicks during the ascent-phase the variance is predominantly low, with a few whales having a higher variance of roll. These two outliers with a high variance of roll when the whale is not clicking are the only two out of the 25 whales where the variance higher when the whales are not clicking. Statistically the difference in roll-variance is significantly different, showing that the variance of roll is higher at the remaining 23 of the whales (Wilcoxon non-parametric paired test: Z=-4.184 p=0; n=25; mean $s_{noclicking}$ =

0.2409; mean $s_{clicking}$ = 0.7090). In the Atlantic, the variance of roll shows to be very high for the majority of whales when they are clicking during the ascent, which changes to the almost opposite when they stop clicking, where the whales show to have a predominantly low roll-variance with a few outliers close to 0.5. The difference in how much the roll-behaviour changes whether the whale is clicking or not is shown in the bottom plot, where all whales have been found to have a higher variance of roll when they are clicking, and the difference in variance to be significantly different (Wilcoxon non-parametric paired test: Z=-2.201 p=0.028; n=6; mean $s_{noclicking}$ = 0.2676; mean $s_{clicking}$ = 0.7386). When the whales in the Mediterranean are clicking they all show a relatively high variance of roll, indicating that they are rolling very actively at varied angles when they are producing regular click on their way to the surface. When they stop producing regular clicks, the tendency for the whales to have a very low variance in roll emerges, with only a few outliers, showing a higher variance than the remainder of whales from this location. The difference between when the whales are clicking and when they are not, is found to be significantly different (Wilcoxon non-parametric paired test: Z=-2.803 p=0.005; n=10; mean $s_{noclicking}$ = 0.2025; mean $s_{clicking}$ = 0.8283) with all the whales having a higher variance of roll when they are clicking. The majority of whales in Norway show to have a variance of roll higher than 0.5 when they are producing regular clicks compared to when they are not clicking, the variance is found at 0.5 and at lower. As found in the other three locations, the difference in variance of roll is predominantly higher when the whales are clicking during the ascent-phase. But the difference in variance of roll for the whales in Norway was not found to be significantly different (Wilcoxon non-parametric paired test: Z=-1.859 p=0.063; n=7; mean $s_{noclicking}$ = 0.2813; mean $s_{clicking}$ = 0.6022).

3.4 Discussion

Extensive use of changes in roll orientation is very apparent when you look at the sensor-data from the Dtag along with the dive profile of a sperm whale. Roll seems to be used in a somewhat systematical way, rolling very actively all the way through almost the entire duration of the dives, changing roll-direction continuously as seen in figure 3.1 and 3.2.

The whales in this study were found to have a higher variance of roll orientation when they were producing regular clicks when comparing all the descents and ascents as well as comparing the roll-behaviour within each of the individual whales. Looking at the mean variance found for each of the analysis at each of the four locations, the mean variance was higher when looking at the individual whales seen during both the descent and ascent and again for each of the whales when compared.

Change in variance of roll for the separate dives

It was decided in the very first stage of the analysis, not to use many of the descent phases, because they did not meet the criteria, and the time before the whales started the regular clicks was too short. The dives that were accepted for analysis showed that during the descent, the whales were rolling with a higher mean variance when they were producing regular clicks. This is seen for all the descents both when looking at the individual dives separately as well as looking at the overall pattern for the individual whale. The fact that the number of descents with a higher variance of roll during clicking was either doubled or tripled compared to the number of descents where the variance of roll was lower, indicating that this trend was not just by chance, which was supported by the statistics as well. In quite a number of descents, the whales were found to start clicking as soon as, or very soon after, they left the surface, which was seen primarily for the male sperm whales tagged in Norway (Madsen et al., 2002b, Teloni et al., 2008). This makes sense for the whales at this location to start clicking as soon as they leave the surface, because they do forage at shallower depth than seen for other locations at lower latitudes. The separate descents found in the data from Norway, shows that even though the number of descent with a higher variance of roll when the whales are clicking, are approximately tenfold higher, the actual difference between the roll-variance during 'clicking' and 'no clicking is not that great. They started to produce regular clicks and the search for prey closer to the surface because they know that the prey is present at shallow depth.

As seen with the descent phase, many ascent phases were cut, in this case it was because in a majority of ascents the whales stopped clicking very soon after changing the

pitch swimming upwards toward the surface, as seen in this data set described in Watwood et al. (2006) and in the example mentioned by Zimmer et al. (2003) that the whales stopped clicking very soon after starting the ascent-phase. The opposite situation is found as well, predominantly in Norway where the whales start producing the regular clicks early in the descent, as well, but during the ascent they produce clicks almost the entire way to the surface. As during the descent phase, it is reasonable for them to continue searching for prey, because the prey is present at shallow depths in Norway. These dives, of course, have not been used in the analysis, because of too little time where the whale is not clicking to be compared to when they are clicking.

Change in variance of roll for the individual whales

When including the affect of the individual whale into the analysis, the tendency is not seen to change much from what is found pooling individual dives. A generally higher variance of roll is seen when the whales are clicking during the ascent phase, with a distinct difference in roll-variance between the whales producing regular clicks and the silent time-interval before they surface. The same tendency is shown when the whale stop the clicking on their way to the surface, where the difference in the variance of roll is predominantly high when the whales are clicking, which is seen in the statistical test as well. Compared to the trend during the descent-phase, they are the same, but much more apparent when the whale is clicking and when it is not during the ascent-phase. The strong difference found in the variance of roll during the ascent for all the locations, is partly shown when separating the ascents into locations as well. The Gulf of Mexico and the Mediterranean both show strong difference in variance of roll, with predominantly higher variance when the whales are clicking, same tendency is shown for the remaining two locations, where the Atlantic does show a significant difference in roll-variance as well, though less strong, but with all the whales showing a higher variance of roll when clicking. The majority of whales tagged at the Norway location were found to have a higher variance of roll when the whales were clicking, meaning that they rolled more, though without the difference in roll-variance between ‘clicking’ and ‘no clicking’ showed any significant difference.

The difference in sample size between the four locations has made it difficult to compare the statistics accurately, especially when comparing the variance of roll for the individual whales. The Atlantic, the Mediterranean and Norway all showed low sample sizes as well as a significant difference in the variance of roll, while others did not, even though both the mean-variance, as well as the number of whales showing a high variance of roll was almost exclusively higher than whales showing a low variance.

This would be a reason to pool the data, as done for the separate dives, but as mentioned in chapter 2, this could cause possible complications when pooling the data. Combining data from several whales and then compare the 'clicking' and 'no clicking' within each descent and ascent. The affect of the individual whale is lost, in case of one whale having a preference for having a more diverse rolling-behaviour that would get lost in this way of looking at the data. If the tag from that particular whale had recorded a higher number of dives than average on the tag, this would influence both the overall result and the statistics. Because of the strict criteria set for both the descent and the ascent, many dives have been cut and not used in the analysis, and because of this many dives does not have one or the other of either the ascent or the descent, making each dive possibly less affective on its own to be dominating a preference from one particular whale, affecting the entire result. But to make sure that the result is not biased, and because it would be interesting to see if there is a difference within individual whales.

3.5 Conclusion

So what could be the reason for the sperm whales in this study to show a trend to be rolling more actively when they are producing regular clicks? Numerous studies (Madsen et al. 2002a, Thode et al., 2002, Zimmer et al. 2003) have suggested that the sperm whale is directing its regular clicks for a certain depth during the descent. By adjusting the ICI with depth, meaning that the whale will increase the time-interval between each emitted click the closer it gets to the depth layer or seabed it began clicking at when beginning the descent. In this study, a clear indication is seen that the whales do roll more when they are clicking during the descent. A suggestion could be that when the

sperm whale is searching for prey, the sonar beam is not quite on-axis as suggested by Zimmer et al. (2005), but a number of degrees off-axis, explaining why the whale is showing a more extensive roll-behaviour while producing clicks, because it will widen the cone-shaped search area as suggested for finless porpoises in Akamatsu et al. (2009).

CHAPTER 4: General Discussion

4.1 Vision

What is the function of roll orientation in the diving sperm whale? Because of the highly active use of roll observed in sperm whales on Dtags from four locations, it seems likely that there should be a reason for the whales to use this manoeuvre so constantly throughout the dive.

In this thesis, the aims were to test: 1) the hypothesis by Fristrup and Harbison (2002) that the sperm whale might be using downwelling light during the day to spot prey or prey patches as silhouettes against the lighter sea surface. 2) A second hypothesis by Fristrup and Harbison (2002) suggested that the sperm whales use vision to look for bioluminescence in prey at depth, or during the night when no light is available. 3) that rolling relates to the use of echolocation.

These ideas were tested by using the roll-behaviour from 51 tagged whales at four locations; the Gulf of Mexico, the north Atlantic, the Mediterranean and northern Norway.

Knowledge about sperm whale vision is limited, but the eye-fold above the eye of the sperm whale likely blocks the vision of the whale so it is not able to look upwards, which was assumed in this study. This predicted limitation of their field of vision, made it possible to test the way whales rolled during the day compared to roll-behaviour during the night. The assumption made in this study was that the whales were not able to look upwards when swimming rightside up at angles between ±45º. This meant that when the whale was rolled within the remaining 315º (LURA) they were assumed to be able to see downwelling light from the sea surface during the day. During the bottom-interval the whales were assumed to be dedicating their time primarily to foraging, searching for prey and feeding, indicated by the production of buzzes. The bottom-interval (bottom-phase) was found in Miller et al. (2004b) to be the part of the dive where the highest number of buzzes was produced. The whales in this study were found to be rolled at angles within LURA for the majority of the time while searching at a flat and downwards directed pitch. This tendency is shown in the relationship between the pitch and roll seen in figure

2.4, where the whales were rolled upside down and on the side while swimming at a downwards directed pitch, primarily on the side during the flat pitch and on the side and rightside up when swimming upwards.

Roll does probably play a part in the foraging of sperm whales, but likely not in the use of downwelling light, as whales did not have a higher proportion of roll within LURA during the day, when downwelling light was potentially available, than during the night. No significant difference in proportion of roll angles within LURA was found for day versus night during the search phase within both the Gulf of Mexico and the Mediterranean. The whales seemed to be spending approximately the same amount of time being rolled upside down or on the side during the day as seen at night. The roll-behaviour did change for each of the pitch-modes during the search-phase, indicating that the whale did have some purpose for performing their roll-manoeuvres when they forage. The only day-night difference found was a tendency for whales in the Mediterranean to be rolled at an angle at which they could see upward during the day than the night, but only during buzzes when the animals were pitched flat. By using the pitch and roll to position itself in a better way to catch a prey during the buzzes, which seem to be very stereotypic for all the locations and all depths with the whale being rolled upside down or on the side. When buzzing at a flat pitch, being rolled at angles within LURA may be an advantage during prey capture because of the positioning of the mouth. It might be easier for the sperm whale to catch and eat the prey when the whale was rolled upside down, and could be an advantage in regards to prey escape-behaviour or the way the prey move in the water column.

If the whale were using vision when foraging at night or at depth with no sunlight available, an omnidirectional roll-behaviour would have been expected when they were looking for bioluminescence in the prey which would be visible from most angles against the dark water. And because most of the foraging in sperm whales goes on at depths between 60-1840 meters (Watwood et al., 2006; Teloni et al., 2008) where light is probably limited (Douglas et al., 1998) there is no reason why they should not take advantage of the flashing bioluminescent organs found in 77.5% of its prey species (Clarke et al., 1993). The tagged whales in Norway were seen to change their proportion of roll angles within LURA slightly with depth when they were at flat and upwards

directed pitch. While searching in the shallow bottom-intervals a high proportion of roll angles were inside LURA. At deeper depths, the proportion of roll angles within LURA was lower, indicating an omnidirectional roll-behaviour, which could imply that they did use vision, using downwelling light near the surface and looking for bioluminescence at depth in Norway. The whales tagged in the Gulf of Mexico, the Atlantic and the Mediterranean on the other hand, did not appear to change the proportion of roll angles within LURA with increasing depths while searching in the bottom-interval during the day at all three pitch-modes. An indication that these whales were searching at depths, and not showing an omnidirectional roll-behaviour to look for bioluminescence in prey-items appeared by the lack of change in roll-proportion at all three pitch-modes. Even if the general proportion of roll angles within LURA changes, as seen during the search-phase when the whales were at a upwards directed pitch for the three locations, but most importantly, no change were found between the day and night time proportions of roll angles inside LURA.

4.2 Clicking

Looking into the general search-behaviour of the sperm whale, starting when the whale begins the regular clicks when leaving the surface, and dive into the deep. In this part of the search, pitch does not have an effect because the whale is at a fairly constant descending pitch, until the whale levels out and the pitch exceeds zero degrees, starting the bottom-interval. After the bottom interval, some sperm whales did continue the search-phase into the ascent (Madsen et al., 2002; Watwood et al., 2006; Teloni et al., 2008) again swimming at predominantly upwards directed pitch.

The roll-behaviour during both the descent and the ascent was tested, quantifying the difference in the variance of roll-behaviour when the whale was not clicking as they were leaving the surface and again when they arrived back at the surface after a foraging dive. Akamatsu et al. (2009) found that the finless porpoise performs ‘roll-dives’ with a active use of echolocation, compared to dives where the whale is predominantly at angles between ±30º, indicating a connection between roll, clicking and searching in finless porpoises.

In sperm whales the rolling was almost constant when looking at the data from the Dtag, but showed a clear tendency to be changing when the whales were producing regular clicks, thus having a higher variance of roll when clicking. The fact that the whales tended to be rolling more when they were clicking could indicate that the roll is somehow enhancing the effectiveness of the regular clicks. The changes in roll during ascent and descent may correspond to changes in pointing direction by the whale, as was suggested for the finless porpoise (Akamatsu et al., 2009). Alternatively, it could be that by rolling while producing regular clicks, the sperm whales' search area of the echolocation beam would be larger if the clicks were emitted at an angle off the body-axis, as seen for other odontocetes (Au et al., 1987; Au et al., 1999; Philips et al., 2003; Akamatsu et al., 2009).

4.3 Future work

The way the whale was rolled in each of the pitch-modes during the search-phase, indicate a relationship between the whales' pitch and how the whale was rolled as seen in Appendix A for each of the whales. Another relationship was indicated in Chapter 3, where the whales were found to be rolling more when they produce regular clicks. The connection between these two suggested associations is the amount of rolling depends on the production of regular clicks. When descending the whales have been seen to appear to regulate the ICI with depth (Madsen et al., 2002b; Thode et al., 2002; Zimmer et al., 2003), decreasing the ICI with depth, suggesting that the whale is clicking at a certain depth layer or at the seabed. This has only been shown in the descent-phase, but it would be interesting to look at the change in ICI during the bottom-interval where the whale is searching for prey and where the change in pitch seems more possible to have a purpose. Maybe the whale is chasing a prey or searching for a new depth layer with higher prey density or availability. By testing if the ICI changes with differences in pitch it might show that the whales aim their echolocation as seen during the descent (Madsen et al., 2002b; Thode et al., 2002; Zimmer et al., 2003). Preliminary data analysis shows slight indications of the ICI increasing when the whale is at a downwards directed pitch.

Although difficult, but more measurements of the sperm whale beam pattern, to give a more precise indication of how the echolocation beam is emitted in the sperm whale, possibly shedding more light on the foraging behaviour of this extreme deep diving mammal.

An additional function of roll worth looking into would be if sperm whales use roll when changing direction. This could be tested by looking at the change in heading, which is also collected on the Dtag, and comparing it with roll.

4.4 Conclusion

In this thesis, the analysis did not show convincing support for the hypothesis that the sperm whale was using downwelling light to spot silhouettes of prey or prey patches against the lighter sea surface by being rolled upside down during the day. The night time data showed the same tendency, indicating that the preferred upside down or on the side roll-manoeuvre was most likely related to prey species or depth layer, and not specifically to be able to see the downwelling sunlight. The whales were found to show a difference in roll-behaviour within each of the three pitch-modes, indicating that there is a correlation between the pitch and roll, as seen in Appendix A for all of the whales.

The roll-behaviour during the buzz shows a different trend, with the whale having a high proportion of roll-angles within LURA, being rolled upside down or on the side while buzzing in all three pitch-modes, for all four locations. Indicating that the roll-behaviour during the buzz was very stereotyped, not being related to specific factors like location, pitch-mode or depth or prey.

So when all these results are considered together, the conclusion is that the roll in the sperm whale was probably not used by the whale to be able to use vision during foraging when looking at the data from the tagged whales in the Gulf of Mexico, the North Atlantic, the Mediterranean and northern Norway used in this study.

The whales in this study was found to show a higher variance in roll when they were clicking during the descent and the ascent. This could show that the whales are using roll to enhance the use of the regular clicks, when they are searching during the descent and again during the ascent on its way to the sea surface. Therefore, it appears

that the rolling behaviour of the sperm whale is driven more by the echolocation sensory modality than the vision sensory modality.

References

Akamatsu, T., D. Wang, et al. (2010). "Scanning sonar of rolling porpoises during prey capture dives." Journal of Experimental Biology **213**(1): 146-152.

Amano, M. and M. Yoshioka (2003). "Sperm whale diving behavior monitored using a suction-cup-attached TDR tag." Marine Ecology-Progress Series **258**: 291-295.

Aoki, K., M. Amano, et al. (2007). "Diel diving behavior of sperm whales off Japan." Marine Ecology-Progress Series **349**: 287-287.

Au, W. W. L., R. A. Kastelein, et al. (1999). "Transmission beam pattern and echolocation signals of a harbour porpoise (*Phocoena phocoena*)." Journal of Acoustical Society of America **106**: 3699-3705.

Baird, R. W., M. B. Hanson, et al. (2005). "Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates." Canadian Journal of Zoology-Revue Canadienne De Zoologie **83**(2): 257-267.

Baird, R. W., G. S. Schorr, et al. (2006). Studies of beaked whales diving behavior and odontocete stock structure in Hawai'i in March/April 2006. Olympia, WA, Cascadia Research Collective.

Barreiros, J. P., M. L., et al. (2004). "First record of *Polyprion oxygeneios* (Perciformes: Polyprionidae) for the south-west Atlantic and a northernmost range extension." Journal of Fish Biology **64**: 1439-1441.

Barrett-Lennard, L. G., J. K. B. Ford, et al. (1996). "The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales." Animal Behaviour **51**: 553-565.

Chapman, R. P. and J. R. Marshall (1966). "Reverberation from Deep Scattering Layers in the Western North Atlantic." Journal of Acoustical Society of America **40**(2): 405-411.

Clarke, M. R. (1996). "Cephalopods as prey. III. Cetaceans." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **351**: 1053-1065.

Clarke, M. R., H. R. Martins, et al. (1993). "The Diet of Sperm Whales (*Physeter-Macrocephalus* Linnaeus 1758) Off the Azores." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **339**(1287): 67-82.

Clarke, R. and O. Paliza (2003). "When attacking their prey sperm whales are upside down." Marine Mammal Science **19**(3): 607-608.

Croxall, J. P., G. L. Everson, et al. (1985). "Fur seal diving behaviour in relation to vertical distribution of krill." Journal of Animal Ecology **54**: 1-8.

Davis, R. W., N. Jaquet, et al. (2007). "Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico." Marine Ecology-Progress Series **333**: 291-302.

Denton, E. J. (1990). Light and vision at depths greater than 200 metres. Light and Life in the Sea. P. J. Herring. Cambridge, Cambridge University Press**:** 127-148.

Dietz, R., A. D. Shapiro, et al. (2007). "Upside-down swimming behaviour of free-ranging narwhals." BMC Ecology **7**(14).

Douglas, R. H., D. M. Hunt, et al. (2003). Spectral Sensitivity Tuning in the Deep-Sea. Sensory Processing in Aquatic Environments. S. P. Collin and J. N. Marshall. New York, Springer.

Douglas, R. H., J. C. Partridge, et al. (1998). "The eyes of deep-sea fish I: Lens pigmentation, tapeta and visual pigments." Progress in Retinal and Eye Research **17**(4): 597-636.

Drouot, V., A. Gannier, et al. (2004). "Diving and feeding behaviour of sperm whales (*Physeter macrocephalus*) in the Northwestern Mediterranean Sea." Aquatic Mammals **30**(3): 419-426.

Evans, K. and M. A. Hindell (2004). "The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters." ICES Journal of Marine Science **61**: 1313-1329.

Fristrup, K. M. and G. R. Harbison (2002). "How do sperm whales catch squids?" Marine Mammal Science **18**(1): 42-54.

Gannon, D. P., N. B. Barros, et al. (2005). "Prey detection by bottlenose dolphins, Tursiops truncatus: an experimental test of the passive listening hypothesis." Animal Behaviour **69**: 709-720.

Gaskin, D. E. (1982). The ecology of whales and dolphins. London and Exeter, New Hampshire, Heinemann.

Gaskin, D. E. and M. W. Cawthorn (1967). "Diet and feeding habits of the sperm whale (*Physter catodon* L.) in the Cook Strait region of New Zealand " N.Z. Journal of Marine & Freshwater Research **2**: 156-179.

Gilly, W. F., U. Markaida, et al. (2006). "Vertical and horizontal migrations by the jumbo squid Dosidicus gigas revealed by electronic tagging." Marine Ecology-Progress Series **324**: 1-17.

Goldbogen, J. A., J. Calambokidis, et al. (2006). "Kinematics of foraging dives and lunge-feeding in fin whales." Journal of Experimental Biology **209**(7): 1231-1244.

Hays, G. C. (2003). "A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations." Hydrobiologia **503**: 163-170.

Hucke-Gaete, R., C. A. Moreno, et al. (2004). "Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off southern Chile." Ccamlr Science **11**: 127-140.

Jaquet, N., S. Dawson, et al. (2001). "Vocal behavior of male sperm whales: Why do they click?" Journal of the Acoustical Society of America **109**(5): 2254-2259.

Jaquet, N., S. Dawson, et al. (2000). "Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications." Canadian Journal of Zoology-Revue Canadienne De Zoologie **78**(3): 407-419.

Jerlov, N. G. (1976). Marine optics. Amsterdam, Elsevier Scientific: Amsterdam.

Johnson, M. P. and P. L. Tyack (2003). "A digital acoustic recording tag for measuring the response of wild marine mammals to sound." Ieee Journal of Oceanic Engineering **28**(1): 3-12.

Land, M. F. (1990). Optics of the eyes of marine animals. Light and Life in the Sea. P. J. Herring. Cambridge, Cambridge University Press.

Levenson, D. H. and A. Dizon (2003). "Genetic evidence for the ancestral loss of short-wave length-sensitive cone pigments in mysticete and odontocete cetaceans." Proceedings of the Royal Society of London Series B-Biological Sciences **270**(1516): 673-679.

Madsen, P. T., R. Payne, et al. (2002). "Sperm whale sound production studied with ultrasound time/depth-recording tags." Journal of Experimental Biology **205**(13): 1899-1906.

Madsen, P. T., M. Wahlberg, et al. (2002). "Male sperm whale (*Physeter macrocephalus*) acoustics in a high latitude habitat: implications for echolocation and communication." Behav. Ecol. Sociobiol. **53**: 31-41.

Madsen, P. T., M. Wilson, et al. (2007). "Clicking for calamari: toothed whales can echolocate squid Loligo Pealeii." Aquatic Biology **1**: 141-150.

Mathias, D., A. Thode, et al. (2009). "Relationship between sperm whale (*Physeter macrocephalus*) click structure and size derived from videocamera images of a depredating whale (sperm whale prey acquisition)." Journal of the Acoustical Society of America **125**(5): 3444-3453.

Miller, P. J. O., M. P. Johnson, et al. (2004). "Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture." Proceedings of the Royal Society of London Series B-Biological Sciences **271**(1554): 2239-2247.

Miller, P. J. O., M. P. Johnson, et al. (2004). "Swimming gaits, passive drag and buoyancy of diving sperm whales Physeter macrocephalus." Journal of Experimental Biology **207**(11): 1953-1967.

Mohl, B., M. Wahlberg, et al. (2003). "The monopulsed nature of sperm whale clicks." Journal of the Acoustical Society of America **114**(2): 1143-1154.

Peichl, L., G. Behrmann, et al. (2001). "For whales and seals the ocean is not blue: a visual pigment loss in marine mammals." European Journal of Neuroscience **13**: 1520-1528.

Philips, J.D., P.E. Nachtigall, et al. (2003). "Echolocation in the Risso's dolphin, Grampus griseus." Journal of the Acoustical Society of America **113**(1): 605-616.

Santos, M. B., G. J. Pierce, et al. (1999). "Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996." Marine Ecology-Progress Series **183**: 281-294.

Smith, S. C. and H. Whitehead (1993). "Variations in the feeding success and behaviour of Galapagos sperm whales (*Physeter macrocephalus*) as the relate to oceanographic conditions." Canadian Journal of Zoology-Revue Canadienne De Zoologie **71**: 1991-1996.

Soto, N. A., M. P. Johnson, et al. (2008). "Cheetahs of the deep-sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands)." Journal of Animal Ecology **77**: 936-947.

Southall, K. D., G. W. Oliver, et al. (2002). "Visual pigment sensitivity in three deep diving marine mammals." Marine Mammal Science **18**(1): 275-281.

Teloni, V. (2005). "Patterns of sound production in diving sperm whales in the northwestern Mediterranean." Marine Mammal Science **21**(3): 446-457.

Teloni, V., M. Johnson, et al. (2008). "Shallow food for deep divers: Dynamic foraging behavior of sperm whales in a high latitude habitat." Journal of Experimental Marine Biology and Ecology **354**: 119-131.

Thode, A., D. K. Mellinger, et al. (2002). "Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico." Journal of the Acoustical Society of America **112**(1): 308-321.

Vecchione, M. and C. F. E. Roper (1991). "Cephalopods observed from submersibles in the western north Atlantic." Bullitin of Marine Science **49**(1-2): 433-445.

Wahlberg, M. (2002). "The acoustic behaviour of diving sperm whales observed with a hydrophone array." Journal of Experimental Marine Biology and Ecology **281**: 53-62.

Warrant, E. J., C. P. Collin, et al. (2003). Eye design and Vision in Deep-Sea Fishes. Sensory Processing in Aquatic Environments. S. P. Collin and N. J. Marshall. New York, Springer**:** 303-322.

Watanabe, H., T. Kubodera, et al. (2006). "Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific." Marine Ecology-Progress Series **315**: 187-197.

Watanabe, Y., E. A. Baranov, et al. (2004). "Foraging tactics of Baikal seals differ between day and night." Marine Ecology-Progress Series **279**: 283-289.

Watwood, S. L., P. J. O. Miller, et al. (2006). "Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*)." Journal of Animal Ecology **75**(3): 814-825.

Zar, J. H. (2010). Biostatistical Analysis. New Jersey, Pearson Education International.

Zimmer, W. M., P. L. Tyack, et al. (2005). "Three-dimensional beam-pattern of regular sperm whale clicks confirms bent-horn hypothesis." Journal of Acoustical Society of America **117**(3): 1473-1485.

Zimmer, W. M. X., M. Johnson, et al. (2003). "Combining data from a multisensor tag and passive sonar to determine the diving behavior of a sperm whale (*Physeter macrocephalus*)." Ieee Journal of Oceanic Engineering **28**(1): 13-28.

Appendix A: Pitch/Roll relationship for all the tagged whales

Each of the figures is showing the relationship between the pitch and roll from the individual tagged whales from the four locations: the Gulf of Mexico, the Mediterranean, the Atlantic and northern Norway. The blue plot on the left represents the data points from one individual whale from all dives at depths deeper than 200 m. The plot on the right, showing the red data points illustrates the data points collected from the bottom intervals collectively from all the dives from that particular individual. The individual tag-ID is marked above each figure, with Roll angles showing on the x-axis and Pitch angles on the y-axis.

The Gulf of Mexico

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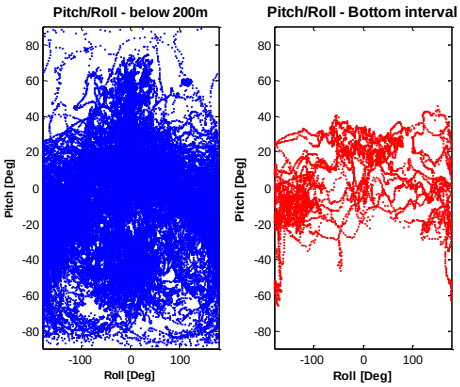

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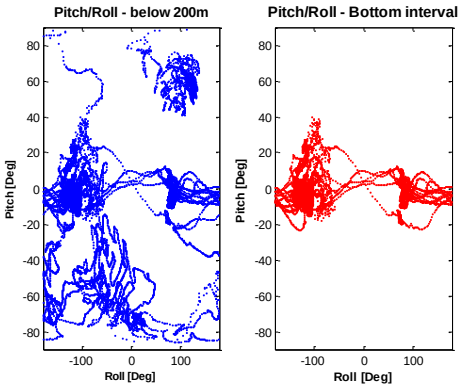

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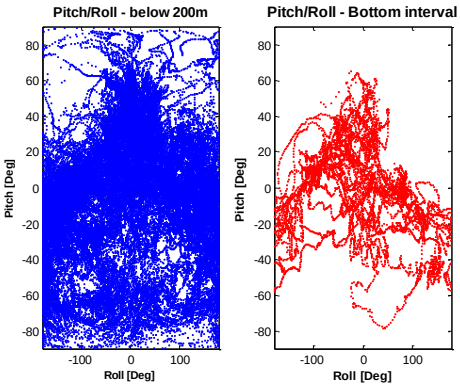

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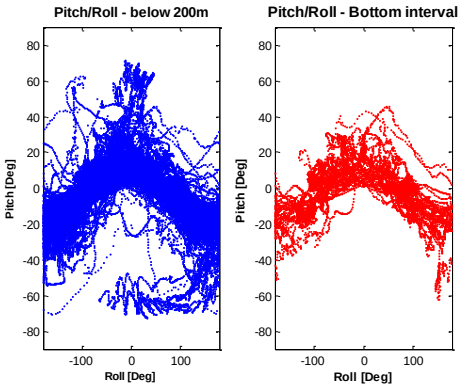

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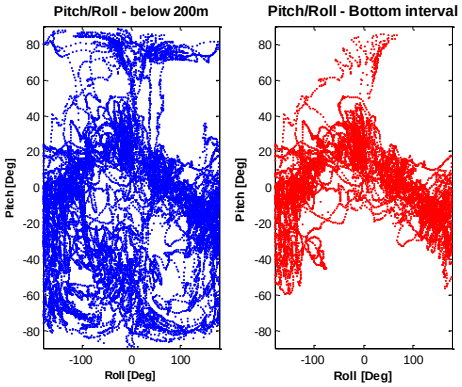

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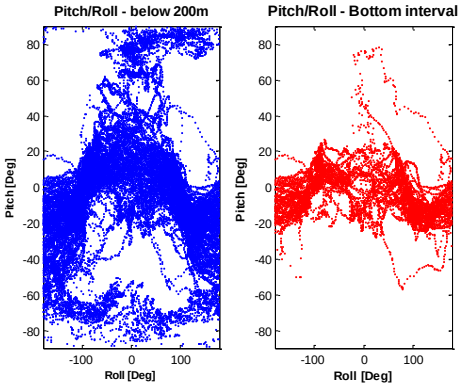

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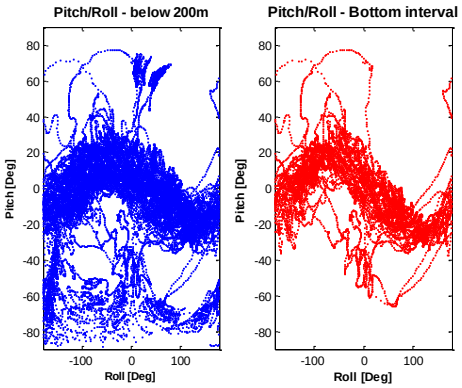

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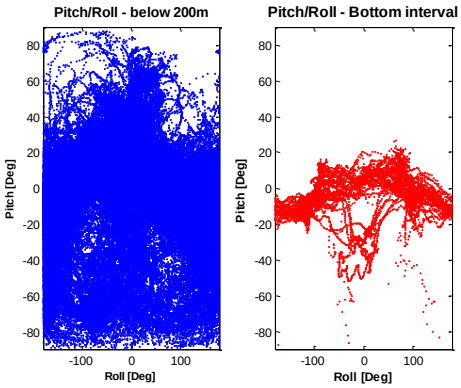

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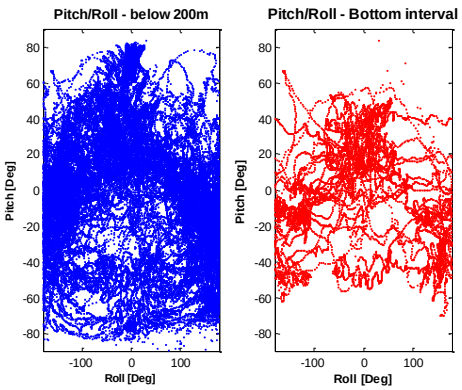

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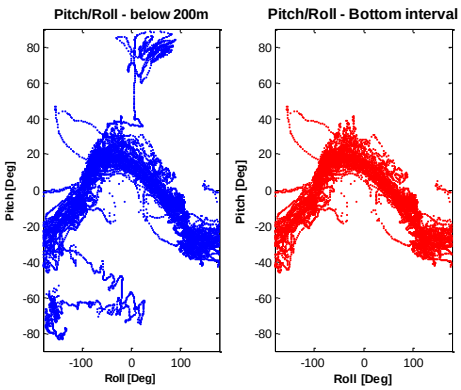

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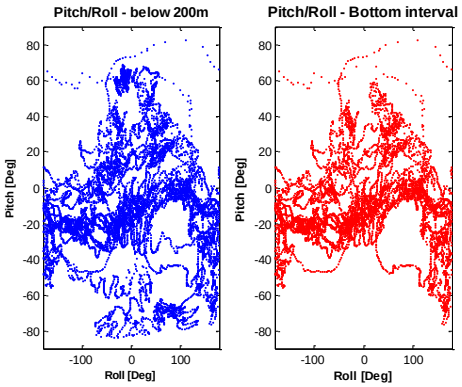

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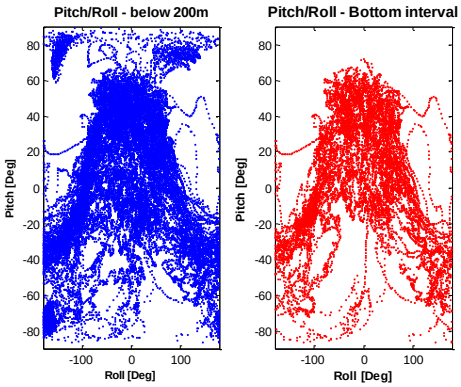

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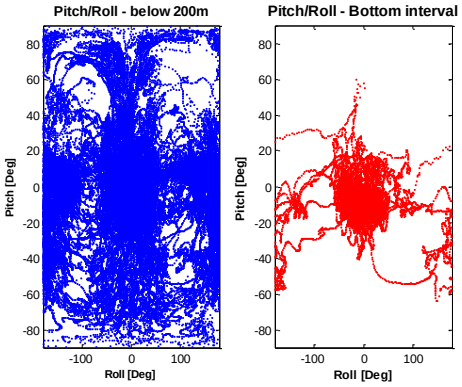

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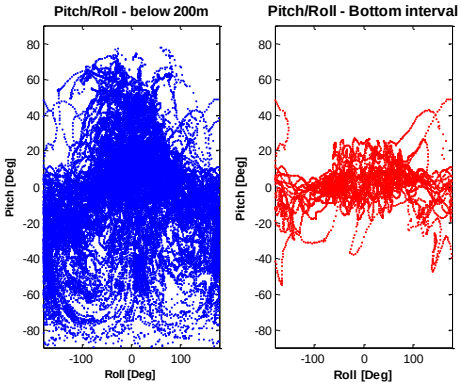

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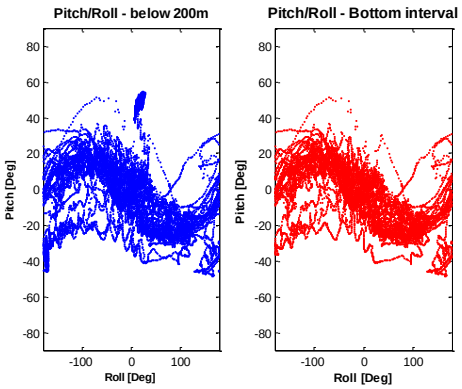

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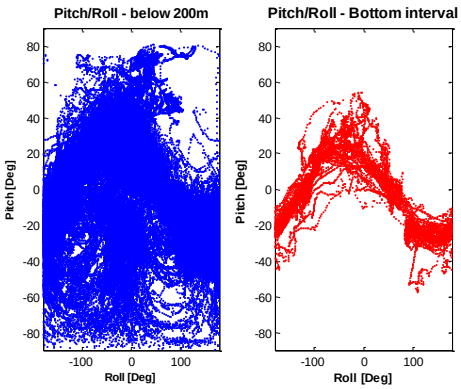

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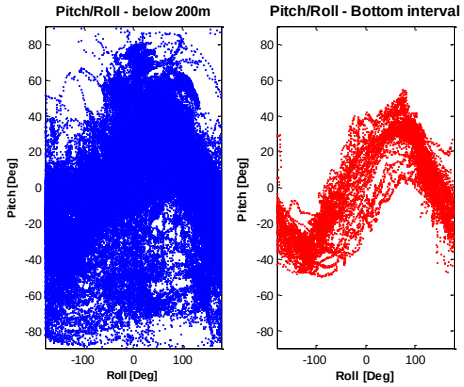

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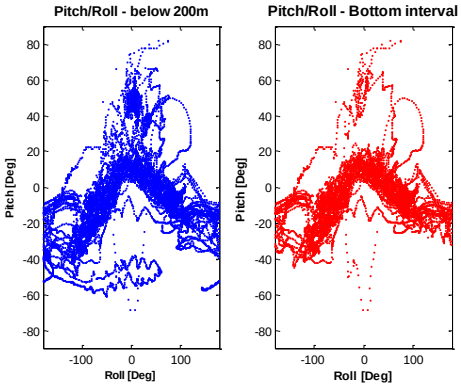

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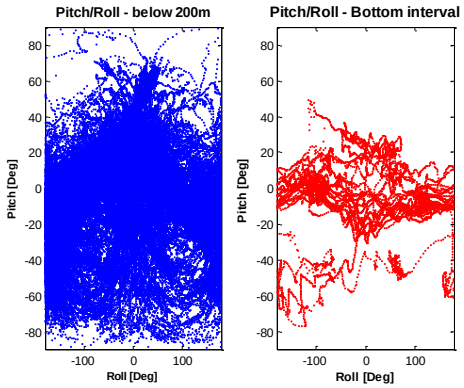

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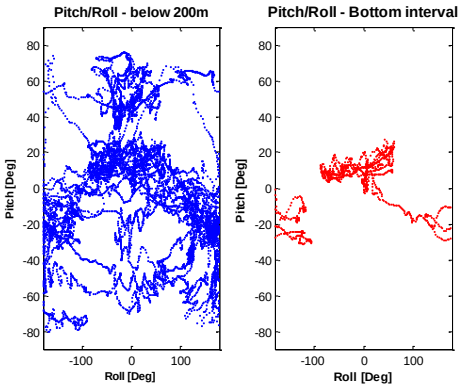

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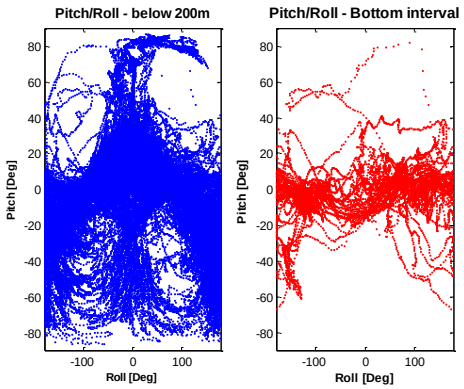

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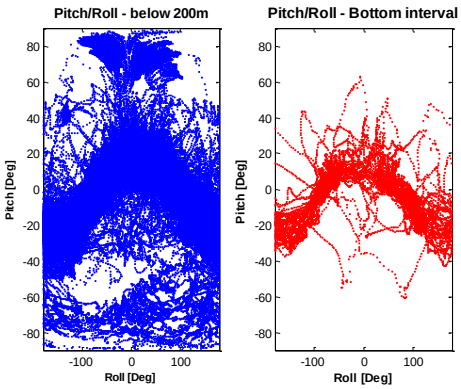

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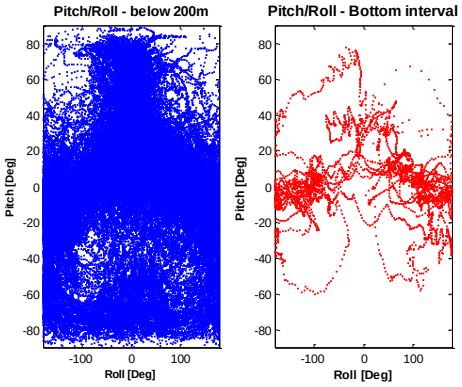

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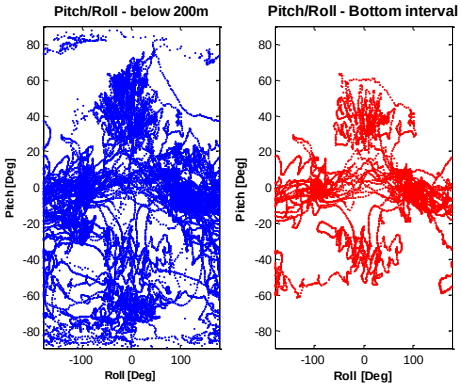

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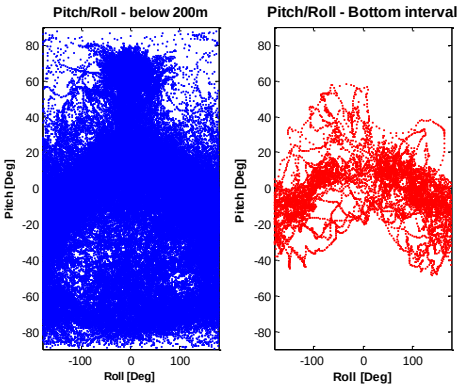

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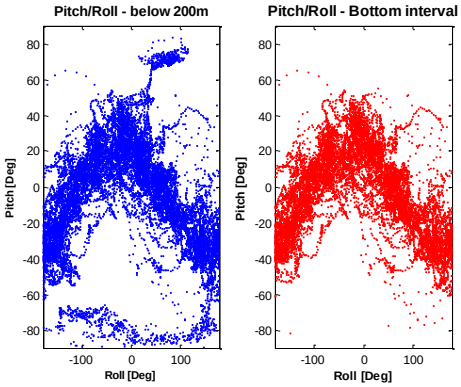
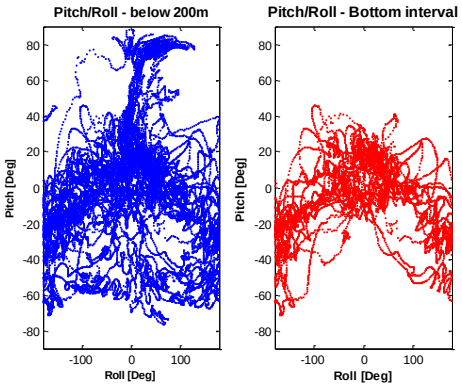


The Atlantic

Sw03_197a



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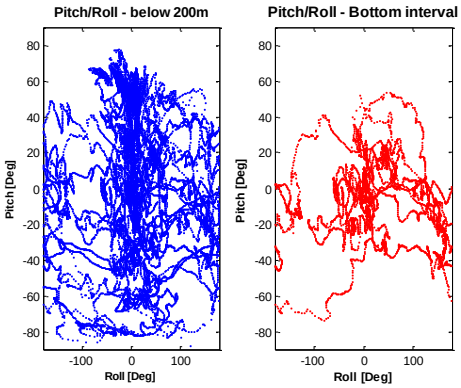

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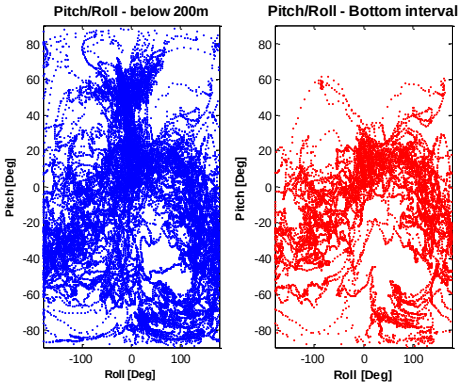

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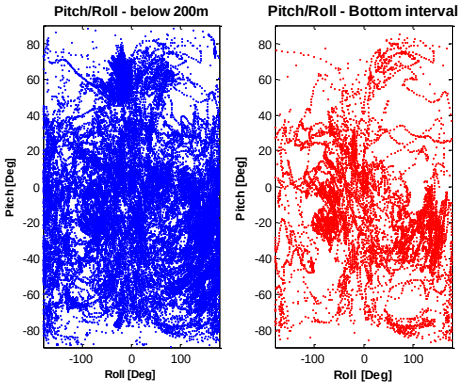

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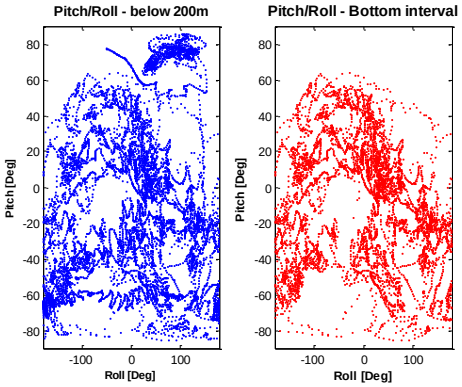

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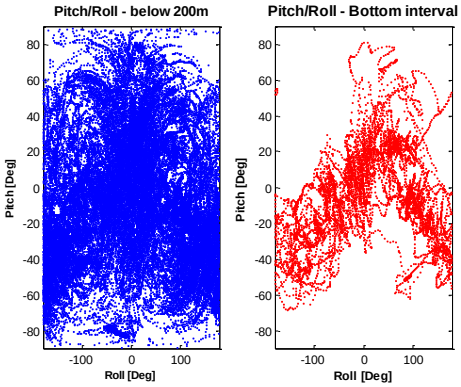

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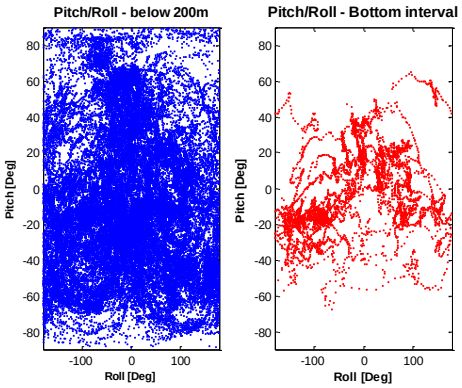
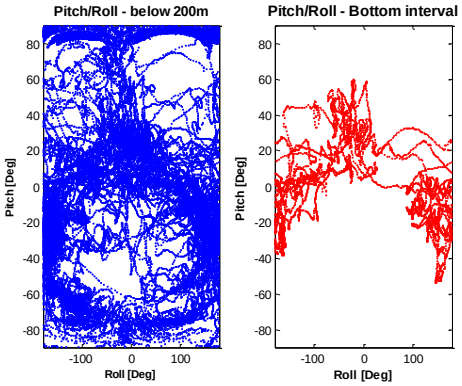
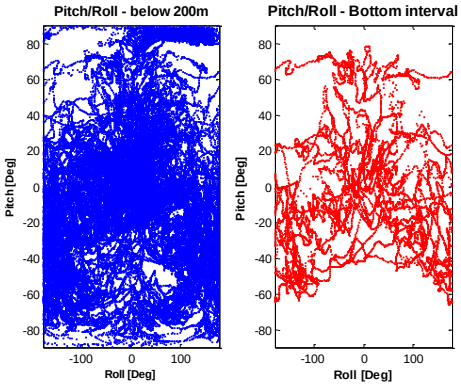


The Mediterranean

Sw01_265



Sw02_191b



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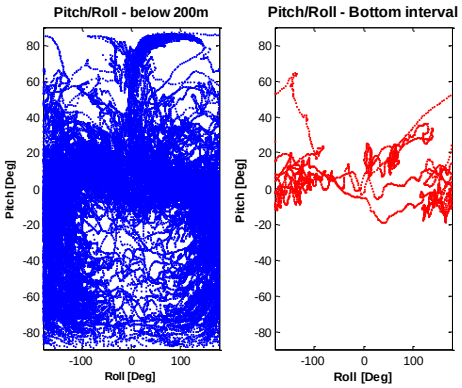

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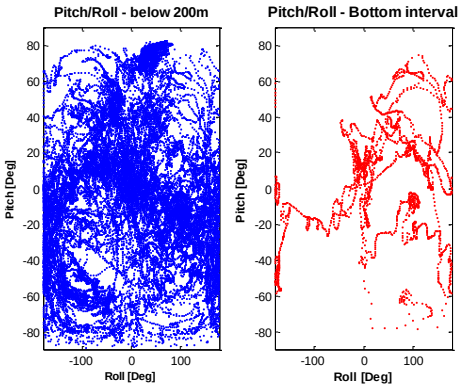

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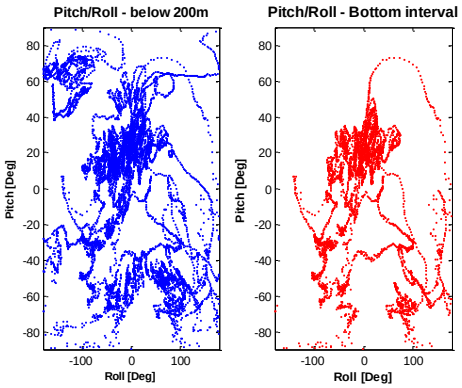

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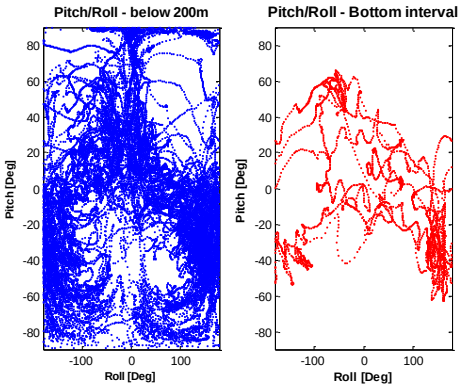

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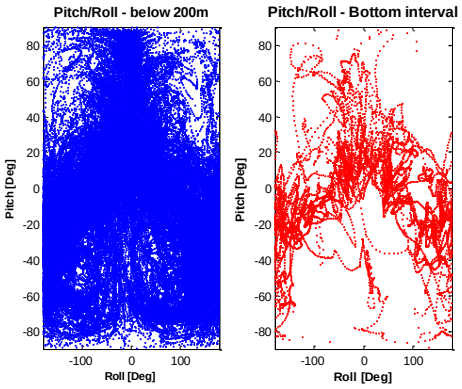

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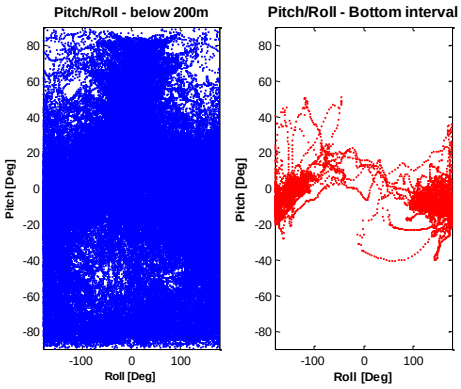

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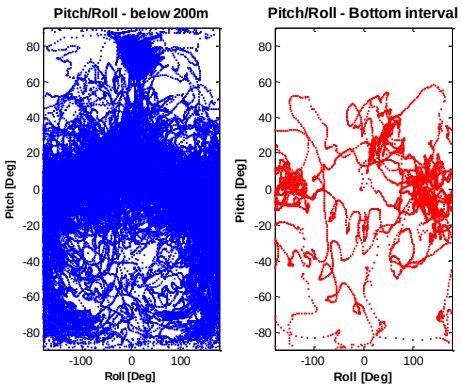

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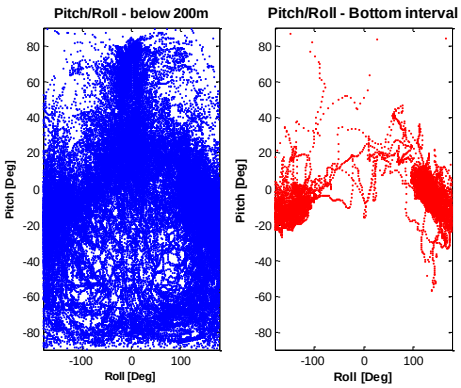

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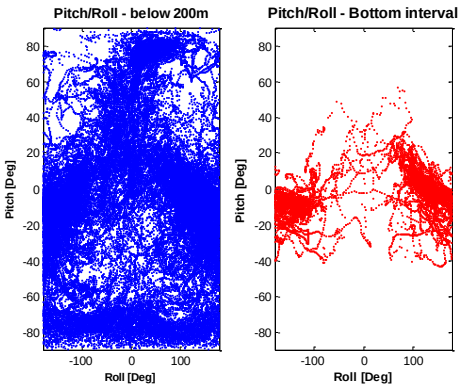
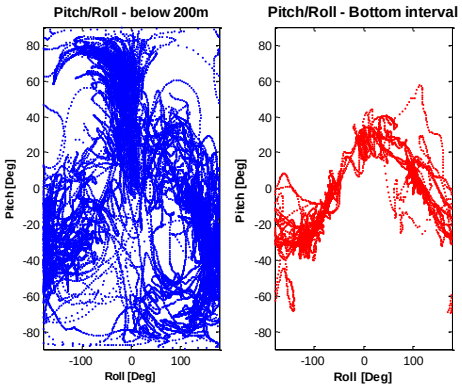


Norway

Sw05_196a



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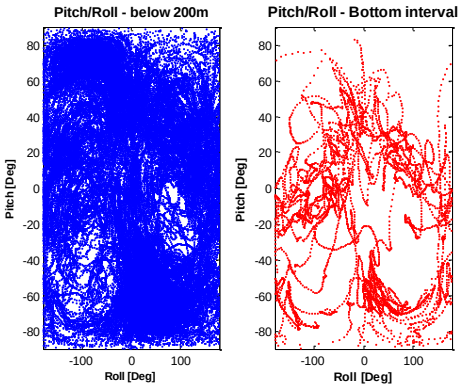

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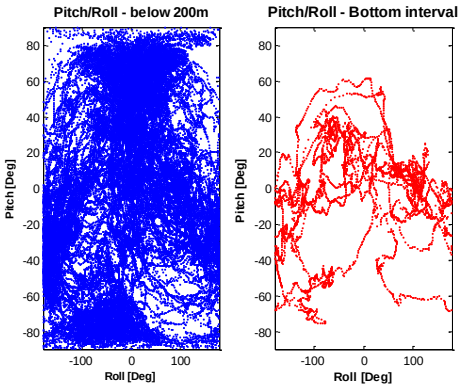

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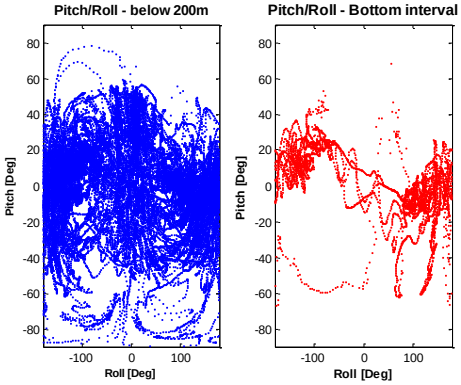

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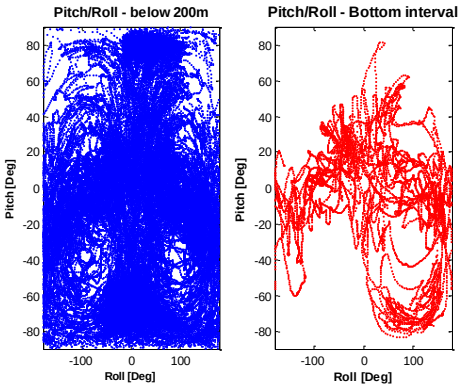

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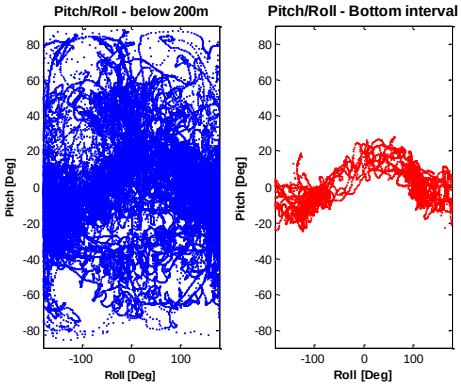

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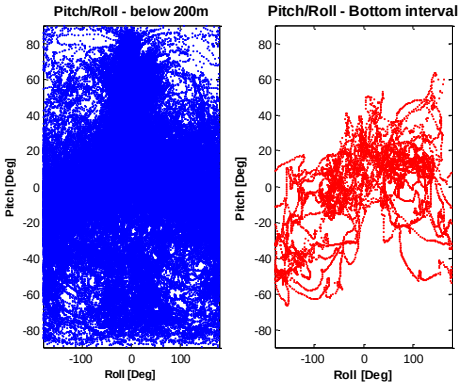
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Pitch/Roll - Bottom interval
Pitch [Deg]
Roll [Deg]
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0
-20
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-60
-80
-100
0
100